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Distribution, Abundance, and Habitat Associations of Franklin's Ground Squirrel (*Spermophilus franklinii* Sabine 1822)

J.J. Huebschman

Illinois Natural History Survey Bulletin
Volume 38, Article 1

February 2007

Illinois Natural History Survey, David L. Thomas, Chief
A Division of the Illinois Department of Natural Resources

Illinois Natural History Survey
Distribution Office
I-Building
1816 South Oak Street
Champaign, IL 61820

Citation:
Huebschman, J.J. 2007. Distribution, abundance, and habitat associations of Franklin's ground squirrel (*Spermophilus franklinii* Sabine 1822). Illinois Natural History Survey Bulletin 38(1):1–58.

Editor: Charles Warwick

US ISSN 0073-4918

Printed by authority of the State of Illinois
P0122452—.75M—02-07

Printed with soy ink on recycled and recyclable paper.

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ABSTRACT

To better inform conservation and management strategies directed at Franklin's ground squirrel, *Spermophilus franklinii*, I reviewed published and unpublished accounts of the squirrel's distribution, abundance, and principally, habitat associations. I present the body of literature on *S. franklinii* and include portions of original accounts to avoid potential bias from paraphrasing. A consensus of the literature indicates that *S. franklinii* is most frequently associated with habitat characterized by a mixture of grassy and woody vegetation, referred to as savanna-like or parkland habitat. Moreover, *S. franklinii* has had an affinity for this type of habitat throughout its geographic range in recent, historic, and even prehistoric times. This is in contrast to a view of the species as primarily associated with tallgrass prairie habitat. As indicated in the literature, populations of *S. franklinii* are subject to marked fluctuations, which probably are influenced by local disturbances in addition to regular dispersal events. In the southern part of its geographic range, *S. franklinii* is currently limited in its occurrence principally to roadside and railroad right-of-ways. In these southern regions *S. franklinii* is justifiably of conservation concern. I suggest that more detailed surveys for the species (such as those that have recently occurred in Illinois and Missouri) take place in Iowa and Kansas.

Keywords: Franklin's ground squirrel, savanna, *Spermophilus franklinii*

INTRODUCTION

Franklin's ground squirrel, *Spermophilus franklinii* (Sabine 1822), is a large ground squirrel, tawny-brown in color, with the exception of both its head and fluffy tail, which are grayish (Fig. 1). The dorsal surface of the squirrel is finely mottled as a result of barring on the shafts of individual hairs that alternates between tawny-brown and black. Hair on the tail, which is long and soft, appears gray because of black and pale-gray barring. Like other North American ground squirrels, *S. franklinii* is both semi-fossorial and an obligate seasonal hibernator (Murie 1999). The annual cycle of *S. franklinii* follows a pattern characteristic of most species of ground squirrels. The ground squirrel cycle begins in spring with emergence from winter hibernacula, and follows with breeding, gestation, lactation, juvenile emergence from natal burrows, fattening prior to hibernation, autumn immergence into hibernacula, and hibernation until the following spring (Michener 1984). The geographic distribution of *S. franklinii* extends from northwest Indiana to north-central Kansas in the south and north through portions of Ontario, Manitoba, Saskatchewan, and Alberta (Fig. 2).

In recent years, interest in *S. franklinii* has increased because of reported declines in some populations (Jones 1964, Schwartz and Schwartz 1981, Johnson and Choromanski-Norris 1992, Benedict *et al.* 1996, Pergams and Nyberg 2001, Martin *et al.* 2003). These declines largely have been reported from the southern, and particularly the southeastern, portion of the squirrel's geographic range. As a result of declining populations, *S. franklinii* warranted an account in the 2003 Red List produced by the World Conservation Union (IUCN), where it was listed as "Vulnerable" (Pergams and Nyberg 2003). Currently, *S. franklinii* also is listed as State-Endangered in Indiana (*in writ.*, Indiana Department of Natural Resources Wildlife Diversity Section 2004), State-Threatened in Illinois (*in writ.*, Illinois Endangered Species Protection Board 2004), and of Special Concern in Missouri (*in writ.*, Missouri Natural Heritage Program 2005) and Wisconsin (*in writ.*, Wisconsin Natural Heritage Working List, 2004).

According to Murie (1999), *S. franklinii* continues to be one of the least known of the North American ground squirrels. This fact is attributable, in part, to the squirrel's habit of occurring in areas of thick vegetation (Jones *et al.* 1983), which inhibits notice and observation of the animal—a fact that also contributes to the dual problem of accurately surveying for the animal and detecting declining populations. I first observed *S. franklinii* in small fragments of tallgrass prairie in eastern Nebraska and, after reviewing the most recent mammalian references for this region (Jones *et al.* 1983,

Figure 1. Franklin's ground squirrel, *Spermophilus franklinii*. Photo courtesy of Jim Rathert, Missouri Department of Conservation.

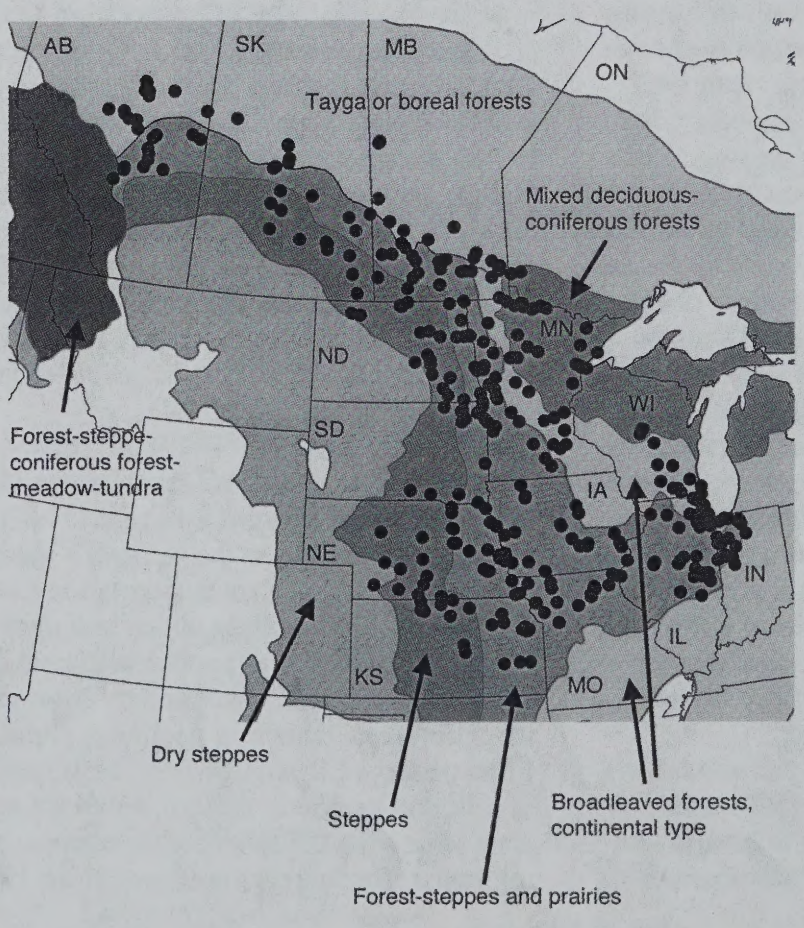

Figure 2. Geographic range map of *S. franklinii* based on a plot of capture localities for 732 museum specimens. The localities of museum specimens examined were converted into latitude and longitude coordinates, when not already given as such, by locating the collection sites on maps or in gazetteers. Bailey's (1998) ecoregion provinces for North America that occur within the geographic range of *S. franklinii* are labeled and overlaid on the map. States and provinces within the geographic range of *S. franklinii* are also labeled. Specimens examined are given in the Appendix.

1985), believed *S. franklinii* to be restricted primarily to tallgrass prairie environments. Jones (1985, p. 157) stated, "A species of the tall-grass prairie, Franklin's ground squirrel must be much less abundant than it was prior to breaking the prairie for agriculture." My views of *S. franklinii* as a species closely associated with the tallgrass prairie did not change until I reviewed all available literature concerning the animal, which was widely scattered, often fragmentary, and in some cases, unpublished. In contrast to my initial views, the available literature suggests *S. franklinii* is an animal primarily of savanna-like habitats, that is, habitats with both a grassy and woody component. My experiences live-trapping *S. franklinii* throughout its geographic range confirm this conclusion. Admittedly, this revelation is largely personal, as persons sharing the squirrel's northern distribution have long considered *S. franklinii* a "brushland" species. However, the perception of *S. franklinii* as a mammal closely tied to prairie habitat remains prevalent in the most recent literature focused on the conservation of the species (Pergams and Nyberg 2003, NatureServe 2004).

Here I present the results of a comprehensive literature review I undertook on *S. franklinii*. I focus principally on the habitat associations of *S. franklinii*, and secondarily on geographic distribution and abundance. Comments summarizing these facets of *S. franklinii* biology and their relevance to the conservation issues surrounding *S. franklinii* are presented in the "Discussion" section.

One purpose of this review is to provide a complete and readily accessible source of information on *S. franklinii* for wildlife biologists, regional land-managers, and others engaged in making decisions that may affect the conservation and management of the species. In addition to practical management applications that may be garnered from this review, it also is my hope that further work on *S. franklinii* will be conducted in order to fill in regional gaps in knowledge about this species; surveys to document extant populations of *S. franklinii* in Iowa, Kansas, southern Minnesota, and South Dakota are a place to start. Finally, I hope this review will inspire much-needed basic ecological research on *S. franklinii*. For example, what factors limit the squirrel's geographic range? How are habitat components actually utilized and what factors are responsible for population fluctuations? In the next few decades it should no longer be said that *S. franklinii* remains one of the least known of North American ground squirrels.

METHODS

I reviewed both published and unpublished materials. Unpublished materials included early reports of U.S. Biological Survey field personnel archived in the Smithsonian's National Museum of Natural History (NMNH). All archived sources are from Series 1 and 2 of Record Unit 7176, United States Fish and Wildlife Service, Field Reports from 1860–1961. I provide box and folder numbers for all individual references obtained from NMNH archived sources. Unpublished material also included state and federal reports, graduate theses, and information on museum specimen tags. Patterns of distribution, abundance, and habitat association of *S. franklinii* were reviewed by state and province in a chronological fashion from the oldest records to the most recent, in order to facilitate ease in finding information on a specific region. An account of *S. franklinii* from the late Pleistocene and Holocene was also included. Portions of original accounts were included throughout this review in order to avoid potential bias from paraphrasing.

ACCOUNTS

Pleistocene and Holocene

Eshelman and Hibbard (1981) tentatively reported *S. franklinii* from the Nash local fauna in Meade County, Kansas, on the basis of two teeth. Their site is bracketed between two layers of volcanic ash dated at 1.2 and 1.9 million years before present (YBP). Evidence suggests that this site was characterized by semi-arid prairie with cool habitat along a stream (Eshelman and Hibbard 1981). If accurately identified, the material from the Nash local fauna would represent the oldest records of *S. franklinii* of which I am aware.

The southernmost records of *S. franklinii* fossil material come from sites in northern Texas. Griffin (1989) reported *S. franklinii* from the Patterson Ranch local fauna in Knox County, Texas—a site from the middle of the Pleistocene Epoch dated at 600,000 YBP. Hibbard and Dalquest (1966) tentatively reported *S. franklinii* from the Vera local fauna, Knox

County, Texas—a site contemporaneous with the Patterson Ranch local fauna. Hibbard and Dalquest (1966) described the climate of the paleo-environment at their site as moist, subhumid, and frost-free.

Rhodes and Semken (1986) reported *S. franklinii* from sites in Mills County, Iowa, during the Wisconsinan, towards the end of the Pleistocene (Table 1). They described the late-Pleistocene habitat of this region of Iowa by stating, "Structurally, the vegetation probably was a parkland like that found today near the forest border in southern Manitoba and Saskatchewan" (Rhodes and Semken 1986, p. 109). They later continued (p. 123), "The Wisconsinan fauna best represents a mosaic of boreal hardwoods and conifers distributed in an open, meadowlike grassland or parkland during much of the glacial period."

Slaughter and Hoover (1963) documented that *S. franklinii* still occurred as far south as northeastern Texas, approximately 650 km south of its current southern limit, during the late Pleistocene. They recorded it in the Ben Franklin local fauna, a site dated at approximately 9,000 – 11,000 YBP in Delta County, Texas (Slaughter and Hoover 1963). The paleo-environment of the site was characterized by numerous large marshes that bordered shallow streams of cool water (Slaughter and Hoover 1963). The most southwestern location of *S. franklinii*, from Beaver County in the Oklahoma Panhandle, also was recorded from a late Pleistocene site (Dalquest and Baskin 1992). According to Dalquest and Baskin (1992) the Elm Creek Site where *S. franklinii* was found "may have offered concealing cover bordering the zone of riparian woodland marginal to the stream" (p. 16). The Elm Creek Site was dated at approximately 11,000 YBP (Dalquest and Baskin 1992).

Although represented in the late Pleistocene, occurrence of *S. franklinii* in the fossil record increased during the Holocene (Table 1), principally in the lower Midwest. In most cases, *S. franklinii* material was associated with habitat consisting of woodland edges and openings (Purdue and Styles 1987) or occasionally riparian woodlands along glacial streams (Dalquest and Baskins 1992).

Within the last 1,000 – 1,500 YBP, *S. franklinii* has been found in association with human settlements. At the Phipps and Brewster cultural sites in western Iowa, Rhodes and Semken (1986) noted a high incidence of the plains pocket gopher, *Geomys bursarius*, along with both the thirteen-lined ground squirrel, *S. tridecemlineatus*, and *S. franklinii*. These species "could have been systematically harvested both for subsistence and in an attempt to mitigate their impact on garden plots" (Rhodes and Semken 1986, p. 117).

North America

Coues and Allen (1877) provided comments on *S. franklinii* that pertained to the species throughout its entire geographic range in North American (Fig. 2). Unfortunately, much of the geographic information they presented was not accurate (see information in the Missouri account). However, their account does provide insight into the historic habitat associations of *S. franklinii*. They stated that it "has a greater preference for thickets, low bushes and borders of timber" than *S. tridecemlineatus* (Coues and Allen 1877, p. 883). They also stated "though a common animal of the prairies of northern Illinois and Wisconsin, it was unknown even to Audubon and Bachman, as late as 1851" (Coues and Allen 1877, p. 882). More recently, Hall and Kelson (1959) quite succinctly stated that *S. franklinii* "occurs in areas of dense high (10 inches or more) grass or weedy vegetational cover and not on closely grazed or mowed fields" (p. 351). Murie (1999) provided an excellent summary account of the species for North America. He noted that they are found in "tall grass in disturbed areas, shrubland, and woodland edges" (p. 419) and that they are sporadically distributed, usually in small colonies, but occasionally with larger populations occurring near marshlands.

In recent reports focused on the conservation status of *S. franklinii* in North America, the species was listed as "Vulnerable" (Pergams and Nyberg 2003) and "Secure" (NatureServe 2004). (The NatureServe assessment of *S. franklinii* was last reviewed in 1996 (NatureServe 2004), prior to the evaluation done by Pergams and Nyberg (2003).) The assessment of Pergams and Nyberg (2003) "is based on declines in area of occupancy and extent of occurrence of *S. franklinii* of > 30% over both the past 10 years, and projections that these declines will continue over the next 10 years. Note is also taken of the extent of loss of the primary habitat of *S. franklinii*: tall- and midgrass prairie" ("Justification" section of Web document). The authors of the Nature-

Serve document state of *S. franklinii*'s habitat use: "Has a strong affinity for tallgrass prairies and the 'edge' between open areas and weeds. Also uses riparian areas (marsh edges), fields, and hedgerows. Generally avoids shortgrass habitats" ("Ecology and Life History" section of Web document). Those authors also suggest that the geographic range of *S. franklinii* may presently be larger than in historic times but likely is occupied by an overall smaller population (NatureServe 2004). Pergams and Nyberg based their ranking, in part, on results from a telephone/e-mail survey of state and provincial mammalogists in which they asked questions concerning the status of *S. franklinii* in their regions.

Canada

Sowls (1948) provided a general review of *S. franklinii* in Canada, where the species reaches the northern limit of its geographic distribution (Fig. 2), from his own observations and those of others, particularly J. Dewey Soper. In an unpublished manuscript cited by Sowls and written by Soper in 1941 (that I could not locate), Soper stated that *S. franklinii* was "essentially an animal of the Transition Zone of the aspen parklands found between the treeless plains and the Canadian Zone forest" (*in* Sowls 1948, p. 115). Soper also stated that in southern Manitoba and northwest of that region, *S. franklinii* inhabited "the aspen poplar groves of the prairie, as well as the wooded lake ridges and the stream and marshland borders" but was "absent from the treeless and scrubless areas" (*in* Sowls 1948, p. 115).

More recently Banfield (1974) reiterated these earlier observations when he summarized the ecology of *S. franklinii* in Canada. He stated: "Franklin's ground squirrels inhabit wooded areas and the edges of woods. They are abundant in poplar bluffs of the aspen parkland that lies between the Great Plains and the coniferous forest. They have even penetrated the coniferous forest belt along the alder banks of streams and the patches of poplars in the evergreen forests, and frequently hunt in marshy areas that lie close to wooded ridges" (Banfield 1974, p. 126). Banfield (1974) stated that populations of the species fluctuate dramatically and average populations in good habitat range from 1.6 to 2.1 animals per hectare.

Alberta. Franklin's ground squirrel reaches the northwest limits of its geographic range in Alberta (Fig. 2). Records indicate that in Alberta *S. franklinii* has been associated most commonly with aspen parkland habitat where it ranges from locally abundant to absent (Table 2). In addition to the accounts cited in Table 2, other sources supplement the current knowledge of *S. franklinii* in Alberta. The earliest account of the species from the province known to me comes from J. Alden Loring from 1894. Loring's account (*in lit.*, NMNH archives, Box 117, Folder 5) from September of that year from "South Edmonton" stated, "A single specimen was taken a short distance from town" and "They are said not to be very common."

During the 1960s and to a greater extent the 1970s, several publications appeared that tangentially referenced the occurrence of *S. franklinii* in Alberta. These included publications on the food habits of raptorial birds (Meslow and Keith 1966, McInvaille and Keith 1974) and on the parasites of ground squirrels (Hilton and Mahrt 1971, 1972; Tobon *et al.* 1976). For the purpose of this review, these studies simply provide evidence of the occurrence of *S. franklinii* in Alberta at a particular place and time. Three of these studies indicated the presence of *S. franklinii* in the vicinity of Rochester, which is about 96 km north of Edmonton (Meslow and Keith 1966, McInvaille and Keith 1974, Tobon *et al.* 1976). Hilton and Mahrt collected *S. franklinii* from the Innisfree area (Hilton and Mahrt 1971) and from four sites in central Alberta (for which they provided a map only with no specific locations); three sites were located between Edmonton and the Saskatchewan border, and one was located roughly between Edmonton and Calgary (Hilton and Mahrt 1972).

Keith and Cary (1991) reported on population trends of *S. franklinii* that they observed coincident with a study on population cycles of snowshoe hare, *Lepus americanus*, conducted in the Rochester area during 1965–1975. They set unbaited traps along *L. americanus* runways in blocks of primarily aspen (*Populus tremuloides*) forest (Keith and Meslow 1966). During the course of their study, 236 *S. franklinii* were captured as incidental species. The primary incidental capture among mammalian species was the red squirrel, *Tamiasciurus hudsonicus*, which was caught 1,820 times (Keith and Cary 1991), further indicating the wooded nature of

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Table 1. Late Pleistocene (until 13,000 YBP) and Holocene (13,000 YBP to current time) sites from the Midwest where Franklin's ground squirrel, *Spermophilus franklinii*, material was recovered. Descriptions of the hypothesized habitat at the site are included when available.

Site name	Location	Estimated time period (YBP)	Hypothesized habitat	Reference
Craigmile	Mills Co., IA	23,240 +/- 535	"The high relative frequency of meadow and grassland ecotypes indicates that extensive boreal grasslands, primarily moist meadows, dominated the landscape. The remaining taxa show that mixed groves of deciduous and coniferous trees with their brushy margins persisted on favorable exposures and provided a weak mosaic of boreal and cool/mesic habitats" (p. 108).	Rhodes and Semken 1986
Waubonsie	Mills Co., IA	14,800 +/- 1000	Boreal grasslands with increased brushland and forest edge.	Rhodes and Semken 1986
Kimmswick	Jefferson Co, MO	12,000–11,000	Cultural site. Species indicate a mix of open and closed, forested habitat.	Purdue and Styles 1987
Elm Creek	Beaver Co., OK	11,410 +/- 410	"The Elm Creek Site may have offered concealing cover bordering the zone of riparian woodland marginal to the stream" (p. 16).	Dalquest and Baskin 1992
Modoc Rock Shelter	Randolph Co., IL	10,000–8,500	Some species indicative of open habitat, but the majority are associated with forest or forest edge.	Purdue and Styles 1987
Dows	Franklin Co., IA	9380 +/- 130	Cool, moist, open deciduous forest with more effective precipitation than today.	Semken and Falk 1987
Cherokee Sewer site, Horizon I	Cherokee Co., IA	6,350	Upland prairie with a gallery forest along major watercourses.	Rhodes and Semken 1986
Coffey	Pottawatomie Co., KS	5163–5270	Most species at site associated with eastern forests. Floodplain forests present, attested to by *Celtis* sp. (hackberry), *Fraxinus* sp. (ash), *Ulmus* sp. (elm), Acer sp. (maple or boxelder), *Populus* sp. (cottonwood), and *Salix* sp. (willow). Upland forest was reduced and replaced with short or mixed-grass vegetation.	Davis 1987
Rainbow site, cultural horizons A & C,	Plymouth Co., IA	A = 1760–1695 C = 1410–1350	For both time periods habitat consisted of woodlands, stream, stream-edge and grassland characterized as tallgrass parkland.	Rhodes and Semken 1986

Table 1 contiued

Site name	Location	Estimated time period (YBP)	Hypothesized habitat	Reference
Oakwood Lakes	Brookings Co., SD	1650–1050	A long-term woodland occupation. Grassland association.	Semken and Falk 1987
Pleasant Ridge	Mills Co., IA	1450 +/- 90	More arid than modern Missouri Valley.	Rhodes and Semken 1986
Phipps	Cherokee Co., IA	1140–600	Complex, multicomponent village. Mesic.	Rhodes and Semken 1986
Brewster	Cherokee Co., IA	1025–750	Gallery forest, prairie, marsh, permanent water. Cultural site.	Rhodes and Semken 1986
Wittrock	O'Brien Co., IA	980–525	Floodplain village.	Rhodes and Semken 1986
Chan-ya-ta	Buena Vista Co., IA	900	Prairie association.	Rhodes and Semken 1986
Solomon River	Mitchell Co., KS	860 +/- 80	Small farming hamlet in a mesic grassland setting.	Davis 1987
14ML15 Glenwood	Mills Co., IA	852–698	Village and nonvillage. "A cool, damp environment, which supported both meadows and forests, was present on the floodplains; valley slopes were characterized by well-drained woodlands which graded upslope into a shrubby zone and finally into an upland prairie" (p. 120).	Rhodes and Semken 1986
Bill Packer	Sherman Co., NE	850–750	Similar to following account.	Semken and Falk 1987
Schmidt	Howard Co., NE	830–790	Central Plains Tradition earth lodge village. "The Schmidt l.f. is most representative of a riverine community with an open gallery forest/meadow association along the flood plain, bordered by a tall-grass prairie on the slopes and a shorter-grass prairie on the uplands" (p. 209).	Semken and Falk 1987
Cahokia	St. Clair Co., IL	800–400	Information not available.	Purdue and Styles 1987
Milford	Dickinson Co., IA	250	Information not available.	Rhodes and Semken 1986

Table 2. Notes on Franklin's ground squirrel, *Spermophilus franklinii*, in Alberta.

Locality	Habitat	Abundance	Citation
Edmonton area	"They frequented brushy tracts and the borders of cultivated fields" (p. 165).	"It is abundant along the road from a few miles north of Edmonton, Alberta to Sturgeon River" (p. 165).	Preble 1908
Alberta general	"we had a glimpse of a Franklin's ground squirrel as it scampered into an aspen bluff beside the trail" (p. 103) "several sources indicated that it was more likely to occur on the brushy wet slopes of Pleasant Valley than anywhere else" (p. 107) "I had also reports of its occurrence in the region of Raft Lake, where it visits the portable graineries drawn up near the woods" (p. 107).	"at Isaly is nearly absent" (p. 106).	Soper 1921
Alberta general	"The more common tracts of occupation are located in poplar 'bluffs' and shrubby grasslands of scattered prairies in park-lands of the Transition Zone. It also invades grassy forest glades, borders of fields and meadows, dry marshes and sloughs, roadsides and railway tracks" (p. 142).	"In some parts of Alberta they are tolerably common, but local dispersal is often spotty with noticeable scarcity, or apparent absence, in different localities" (p. 143). "The species appears to be slowly extending its range west and north with the expansion of settlement" (p. 142).	Soper 1964
Miquelon Lake Park Prov.	area around the garbage pit, surrounded by aspen woodland habitat	"Density of adults varied between 1.25 and 2.50 per ha (0.4 to 0.8 per acre)" (p. 337).	Murie 1973
Alberta general	"aspen parkland belt, especially along the forest edge, where there may be dense grasses" (p. 88).	"It is considered uncommon here but the status is difficult to determine. It may be numerous in some areas...it is not a conspicuous member of the mammal community" (p. 88).	Smith 1993

the study site. Keith and Cary (1991) showed clear fluctuations in the capture rate of *S. franklinii* during their study period, including a time when the population fell "precipitously" (p. 375). The sharp decline in the *S. franklinii* population was roughly coincident with declines in both *T. hudsonicus* and the northern flying squirrel, *Glaucomys sabrinus*, populations. Keith and Cary (1991) reported speculation (from Erlien and Tester 1984—see the Minnesota account) that these declines, which occurred after *L. americanus* declines, may have been the result of prey-switching behavior by predators of *L. americanus*.

Sargeant *et al.* (1993) conducted a study on predators that affect duck production in the Prairie Pothole region, which includes a small portion of Alberta. Throughout this review, I refer to their results as they pertain to *S. franklinii*, which are summarized in Table 3. Their data primarily reflect the occurrence of *S. franklinii* in a particular region with some information on relative abundance (see Table 3). The authors do not provide specific information on habitat use but, instead, present an overview of the physiographic characteristics of all of their study sites. Most (21 of 33) of their study sites occurred in the prairie zone within the Prairie Pothole region, with the remainder (12 of 33) falling within the aspen parkland zone (Sargeant *et al.* 1993). Sites were composed of croplands (average coverage 54%), grasslands (25%), wetlands (13%), woodlands (3%), and additional odd areas or barrens (5%) (Sargeant *et al.* 1993). Cultivated areas included small grains, sunflower, corn, and other row crops (Sargeant et al. 1993). Grassland areas usually were grazed by livestock, and most study areas included occupied or abandoned farmsteads (Sargeant *et al.* 1993). Trees were found in each study area but were most numerous in areas within the aspen parkland zone, where quaking aspen trees (*P. tremuloides*), with hazelnut (*Corylus* sp.) or willow (*Salix* spp.) understory, were prevalent around wetlands and in small woodlots (Sargeant *et al.* 1993). Within the prairie zone, trees were usually in single-row shelterbelts in fields or in multi-row windbreaks at farmsteads (Sargeant *et al.* 1993).

In 1983 Sargeant *et al.* (1993) found *S. franklinii* in Alberta at their Holden and Hay Lakes study sites, both of which were in the aspen parkland zone (Table 3). Relative to other sites in their study (which were located throughout the Prairie Pothole region), at these locales *S. franklinii* was ranked as "scarce" (Sargeant *et al.* 1993, Table 3). Both sites contained woodlots up to 0.65 km^2 (Sargeant *et al.* 1993).

Manitoba. Franklin's ground squirrel has been documented in Manitoba (Fig. 1) since at least 1882 (Seton 1910). It often has been referred to as a common or plentiful species (Bird 1927; Green 1932; Soper 1946, 1961a). However, as Sowls (1948) stated, local populations tend to be variable in size over time (see also Table 4). When present, *S. franklinii* occurs at the interface of woodlands and grasslands where there is often an ecotone composed of various shrubby species (Table 4). In areas of pure grassland, the species is usually limited to isolated patches of woody habitat.

J.A. McLeod (1933) conducted a survey of parasites found in species of *Spermophilus* (then *Citellus*) within Manitoba. Although he provided a thorough review of the parasites, he included virtually no information on the hosts, with one notable exception. For the three species of squirrels he examined (*S. tridecemlineauts*, *S. franklinii*, and *S. richardsonii*), he reported years of peak abundance based on observations of farmers and naturalists within the province. For *S. franklinii*, years of peak abundance occurred in 1912, 1917, 1923, 1927, and 1932 (McLeod 1933). McLeod (1933) also reported that squirrel populations experienced sharp declines between years of peak abundance.

Sowls' (1948) study of *S. franklinii* at Delta Marsh in Manitoba remains one of the most thorough to date. He found *S. franklinii* primarily on a wooded ridge bordering a lake and in small, isolated, tree-covered islands set in stands of reeds, *Phragmites communis*; occasionally, they were found in pure stands of these reeds (Sowls 1948). He reported extreme population fluctuations of *S. franklinii* at Delta Marsh. In 1938, a year of peak abundance, he reported "two boys with .22 rifles were able to kill fourteen in less than an hour without moving from one spot. Such numbers have not been observed since" (Sowls 1948, p. 115). Sowls (1948) wrote that between 1939 and 1942 an observer could see "about six per mile along the ridge road" (p. 115). However, by 1943 they were so uncommon at Delta Marsh

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Table 3. All data presented in the table below are from the study by Sargeant *et al.* (1993) on predators that affect duck production in the Prairie Pothole Region. As in Sargeant *et al.* (1993), study sites marked with an asterisk (*) occur in the aspen parkland zone, those unmarked occur in the prairie zone. Ranks indicate the relative abundance of Franklin's ground squirrels, *Spermophilus franklinii*, at sites as follows: 1=scarce, 2=uncommon, 3=common, and 4=numerous. Percent habitat coverage data are derived from Table 1 in Sargeant *et al.* (1993). Observation rate data are from Appendix Table 10 and data on captures and percent of units with captures are from Appendix Table 11, also in Sargeant *et al.* (1993). Attempts to trap and remove *S. franklinii* occurred only at three study sites, all in Minnesota and North Dakota; those data are from Appendix Table 3 in Sargeant *et al.* (1993). Sargeant *et al.* (1993) utilized 33 study sites, only 31 of those fell within the geographic range of *S. franklinii*, of those, only the 24 where *S. franklinii* was recorded are included in the table below.

		Percent habitat coverage						Franklin's ground squirrels			
Study Site Location	Rank	Cropland	Grassland	Woodland	Wetland	Other	Year	Observation Rate[1]	Captures[2]	Units with captures (%)[3]	# Trapped and removed[4]
CANADA											
Alberta											
Hay Lakes*	1	44	23	10	16	7	1983	6	2	20	-
							1984	0	0	0	-
Holden*	1	45	24	7	17	7	1983	6	2	10	-
Manitoba											
Cartwright	2	66	19	2	7	6	1983	10	0	0	-
Moore Park*	3	62	8	6	14	10	1983	61	9	60	-
							1984	16	23	80	-
Saskatchewan											
Ceylon	1	56	31	0.5	9	3.5	1983	0	1	10	-
							1984	2	0	0	-
Craik	1	84	3	1	7	5	1984	3	0	0	-
							1985	3	0	0	-
Earl Grey*	4	80	2	4	8	6	1985	1	33	30	-
Goodwater	2	50	36	0.5	9	4.5	1983	5	10	40	-
Hanley*	3	70	11	2	11	6	1983	9	42	90	-
							1984	6	45	90	-
							1985	9	25	70	-
Inchkeith*	2	71	10	4	5	10	1984	10	19	50	-
							1985	12	14	40	-
Leask*	1	40	26	16	12	6	1984	1	5	30	-
							1985	0	2	10	-
Shamrock	1	59	29	0.5	7	4.5	1983	0	0	0	-
							1984	0	1	10	-
							1985	2	0	0	-

Table 3 continued

Study Site Location	Rank	Percent habitat coverage					Year	Franklin's ground squirrels:			
		Cropland	Grassland	Woodland	Wetland	Other		Observation Rate[1]	Captures[2]	Units with captures (%)[3]	# Trapped and removed[4]
Yorkton*	2	45	25	14	11	5	1985	6	5	30	-
U. S.											
Minnesota											
Hawley*	1	45	24	12	14	5	1987	0	-	-	-
							1988	1	-	-	-
Hitterdal*	2	61	12	6	17	4	1988	6	-	-	-
Lake Park*	1	57	17	5	17	4	1987	5	-	-	0
							1988	0	-	-	0
North Dakota											
Eldridge	1	81	6	2	9	2	1987	2	-	-	12
							1988	3	-	-	4
Fredonia	1	12	37	0.5	46	4.5	1987	8	-	-	13
							1988	3	-	-	7
Jud	1	58	21	1	14	6	1987	8	-	-	-
							1988	0	-	-	-
Kulm	1	33	43	1	19	4	1988	2	-	-	-
Litchville	1	54	20	2	20	4	1987	3	-	-	-
							1988	0	-	-	-
Sharon	2	79	7	0.5	10	3.5	1983	12	1	10	-
Streeter	1	40	38	0.5	14	7.5	1983	2	4	30	-
South Dakota											-
Parkston	1	47	40	1	7	5	1983	2	0	0	-

[1]=Average number (x 10^3) of places (defined as a 150-m diameter area) per hour one or more individuals were seen.
[2]=Refers to the total number of individuals captured at a study site location in early July in 196–200 trap days (mean = 199.8).
[3]=Refers to percent of 2.6 km^2 units within each study site (10 units per site) in which *S. franklinii* was captured.
[4]=No information on trapping effort is available. Trapping occurred from early April to late June on sites ranging from 63–303 ha.

that a colleague of Sowls' claimed to have seen fewer than a dozen during the course of the summer and in1946 Sowls, himself, recorded fewer than two dozen squirrels during the entire summer.

Iverson and Turner (1972) studied *S. franklinii* at the Whiteshell Nuclear Research Establishment (located approximately 120 km northeast of Winnipeg). Their study population occupied disturbed patches in an old field that was bordered on two sides by aspen forest (Iverson and Turner 1972). Lynch (1972), whose study at Delta Marsh included *S. franklinii* in a suite of predators of duck nests, did not include specific information on the habitat use by the species—although it may be inferred from other accounts of *S. franklinii* from the region (Sowls 1948; Tamsitt 1962). He did provide estimates of density for 1966, stating that *S. franklinii* ranged from 0.69 to 0.93 individuals per hectare (Lynch 1972). Wrigley (1974) found *S. franklinii* to be rare in his study area in the sandhills regions of southwestern Manitoba near Oak Lake and Margaret. Of those *S. franklinii* trapped, three were found by a small maple tree (*Acer* sp.) in an area composed largely of silverberry (*Elaeagnus commutata*) and snowberry shrubs (*Symphoricarpos occidentalis*), and two were found in an area of Saskatoon shrubs (*Amelanchier alnifolia*) (Wrigley 1974).

Two studies on parasites that occurred at Birds Hill Provincial Park in south-central Manitoba provide additional information on habitat associations and abundance of *S. franklinii* in Manitoba (Burachynsky and Galloway 1985, Reichardt and Galloway 1994). Burachynsky and Galloway (1985) caught greater numbers of *S. franklinii* in a study plot composed principally of grasses and shrubs (which were up to 3 m high), bordered by aspen woodland (28 and 30 individuals in 1979 and 1980, respectively), than another study plot composed primarily of aspen woodland, with lesser amounts of habitat in grass and shrubs (16 individuals in both 1979 and 1980). It is worth noting that the aspen woodland was dense enough to provide little understory, due to a large amount of leaf litter and little light penetration (Burachynsky and Galloway 1985). Reichardt and Galloway (1994) captured *S. franklinii* in habitat they characterized as aspen-oak parkland, which included trembling aspen (*P. tremuloides*), bur oak (*Quercus macrocarpa*), and various shrub species. In 1982 these researchers captured 36 individual squirrels (95 total squirrel captures in 552 trap days), and in 1983 they captured 40 individual squirrels (161 captures in 504 trap days).

Sargeant *et al.* (1993) recorded *S. franklinii* from study sites located in proximity to Moore Park and Cartwright in southwest Manitoba (Table 3). In their study, the highest observation rate of *S. franklinii*, out of all 33 study sites, occurred at Moore Park (Sargeant *et al.* 1993). Sargeant *et al.* (1993) ranked *S. franklinii* as "common" at Moore Park, which was in the aspen parkland zone, and "uncommon" at Cartwright, which was in the prairie zone (Table 3).

Hare (2004) studied kin discrimination in *S. franklinii* near Delta Marsh, where the species continues to persist and be utilized as a study organism.

Of note, one early reference about *S. franklinii* in the Aweme area asserted that, "[It] does more harm during the period of its activity than any other member of the genus" (Criddle 1929, p. 157). This statement presumably refers to the propensity of *S. franklinii* to consume agricultural products. Both Sowls (1948) and Lynch (1972) documented *S. franklinii* as a predator of duck nests.

Ontario. The distribution of *S. franklinii* in Ontario is limited to the extreme western edge of the province (Fig. 2), in proximity to both the Manitoba and Minnesota borders. The range of *S. franklinii* appears to have expanded eastward into Ontario within the last century, presumably because of human modifications of habitat, specifically the clearing of land for agriculture (Peterson 1966). Snyder (1938) recorded the first specimens of *S. franklinii* collected from the province. He stated, "Apparently this animal is a fairly recent arrival in the district—certainly it was not present when the area was opened up for agriculture" (p. 169). He reported that the first visual observation of *S. franklinii* in Ontario came from the Rainy River area in June 1925. Snyder (1938) implicated modification of the land in the spread of *S. franklinii* in Ontario when he stated, "As further evidence of its recent arrival it can be said that it is rapidly spreading eastward over cultivated sections. It now [1936] occurs at Emo, which indicates an advance of some twenty-five or thirty miles in seven years" (p. 169). He included *S. franklinii* in a suite of mammals characteristic

of western prairie regions. No specific mention of the habitat surrounding his trapping locations for *S. franklinii* were given, but the area as a whole was a mixture of small agricultural lands set in and among areas characterized by stands of aspen and spruce (Snyder 1938). Peterson (1966) recorded *S. franklinii* from the Kenora, Rainy River, and Fort Francis areas of Ontario, a distribution reiterated by Dobbyn (1994).

Saskatchewan. Franklin's ground squirrel occurs in the southern third of Saskatchewan, excepting the southwest corner of the province (Fig. 2). The original species description of *S. franklinii* was based on specimens collected by Sir John Richardson in Saskatchewan (Sabine 1822). Richardson (1829) described the location where these first specimens were collected by stating, "This animal was seen in the neighborhood of Carlton-house, where it lives in burrows dug in the sandy soil, amongst the little thickets of brushwood that skirt the plain" (p. 168). In 1895, J. A. Loring (*in lit.*, NMNH archives, Box 122, Folder 21) reported *S. franklinii* to be common at Wingard, which—according to his notes—was located approximately six miles (9.7 km) northeast of Carlton-house. He stated, "They were found to be quite thick in the cooleys that run into the river" (*in lit.*, NMNH archives, Box 122, Folder 21). Loring recorded the following information regarding the vegetation of the area: "The country is rolling and covered with patches of thick poplar and quaking asp[en]. Many cooleys run into the river [and] in these may be found two species of poplars[,] *Populus angustifolia* and *Populus tremuloides* besides numerous scrub bushes in which willows predominate. A straggling spruce is found here and there as are also birch trees but they are both rare" (*in lit.*, NMNH archives, Box 122, Folder 22). In the same year, Loring recorded the occurrence of *S. franklinii* at Indian Head in Assiniboia (now southern Saskatchewan). He stated, "Three were taken in Red Fox cooley and several others [were] heard and seen. They seemed to prefer the scrub on the banks of the stream" (*in lit.*, NMNH archives, Box 122, Folder 21) In his vegetation notes of the area he recorded the following, "Indian Head...is situated on a beautiful rolling prairie and is a fine farming district. With the exception of a few bunches of willow here and there, no timber is found outside of Red Fox cooley where *Populus tremuloides* and *Populus angustifolia* are abundant being found in small groves" (*in lit.*, NMNH archives, Box 122, Folder 22). From the earliest accounts of *S. franklinii* in Saskatchewan, this species was associated most commonly with habitat that contained some measure of a woody component either in the form of trees or shrubs. Specimens collected by F. Banfield near Emma Lake (Table 5) in 1939 further illustrate this association.

Soper (1951) reported some of the northernmost records of *S. franklinii* in Saskatchewan, at Prince Albert National Park, and detailed the association of the species with deciduous and coniferous woodlands. He observed two individuals in a small area of black spruce muskeg, others in a poplar woods near open grassland, and found scattered individuals in the "forest-prairie" country in the southern end of the park (Soper 1951, p. 29). Beck (1958) stated that the species was widespread in Saskatchewan, but most abundant in the "bushy regions" (p. 28). In regards to prevalence, Soper (1951), again reporting from Prince Albert National Park, found its distribution "notably inconsistent...in many favourable localities it appeared to be absent" (p. 29). Soper (1961b) reiterated this point a decade later for the region of southern Saskatchewan when he said, "Local dispersal and numbers are noticeably irregular—sometimes common, scarce or apparently wanting" (p. 31).

I gleaned additional information concerning *S. franklinii* in Saskatchewan from the parasitology literature. From May to August in 1976 and 1977, 44 *S. franklinii* were collected near Saskatoon and examined for parasites (Leighton and Wobeser 1978). McGee (1980) examined 46 *S. franklinii* for parasites from Saskatchewan but did not provide additional details on collecting localities. Some of the specimens he examined may have included those collected by Leighton and Wobeser (1978) because the time frame is similar. In 1986 and 1987, Durham *et al.* (1988) examined a total of 13 *S. franklinii*: 11 from the vicinity of St. Denis (40 km east of Saskatoon) and 2 from near the South Saskatchewan River on the outskirts of Saskatoon. None of these parasitological studies provide specific information on the habitat from which the squirrels were collected.

The highest populations of *S. franklinii* found by Sargeant *et al.* (1993) in their study

Table 4. Notes on Franklin's ground squirrel, *Spermophilus franklinii*, in Manitoba.

Locality	Habitat	Abundance	Citation
Manitoba	"Its chief region ...is the poplar country from Pembina to Pelly" (p. 373). "[found] frequenting the edges of thick dry undergrowth near woodlands or along hedges" (p. 373).	"In 1882, we, in Manitoba, reckoned this the rarest of the Ground-squirrels; since then it has increased... while the Striped Ground-squirrel has decreased, so that now this is much the more numerous of the two" (p. 375).	Seton 1910
Spruce Woods Forest & Game Preserve	Found in the deciduous forest community composed almost entirely of aspen (*Populus tremuloides*).	Listed as plentiful, along with other mammals in a long list.	Bird 1927
Manitoba general	"[They] range primarily in the Transition Zone, but overlap into 'pure' Canadian types along the northern fringe of their range in Canada. They are animals of the 'edge.' Their favorite habitat is the area where woods and open country meet" (p. 134).	"population densities are extremely variable over a period of years and cyclic declines and rises are in evidence" (p. 135).	Sowls 1948
Riding Mountain National Park.	"it resorts to habitats in both Transition and Canadian Life zones" (p. 22)	"This species of ground squirrel does not appear to be as commonly dispersed as the two referred to above [*S. tridecemlineatus* and *S. richardsonii*]" (p. 22).	Soper 1953
Delta Marsh	"This species was the only squirrel inhabiting the wooded lake ridges and stream and marshland borders south of Lake Manitoba" (p. 74).	"When trapping started in early June only a few adult animals were present. However, by late July juvenile and young adult animals were seen in large numbers" (p. 74).	Tamsitt 1962

Table 5. Museum specimens of Franklin's ground squirrels, *Spermophilus franklinii*, collected by F. Banfield from Saskatchewan.

Date	Museum	Museum Number	Locality	Collector	Notes from museum tag
1 July 1939	CM	18202	Emma Lake	F. Banfield (#250)	"dry, mixed woods"
5 July 1939	CM	18204	Emma Lake	F. Banfield (#267)	"bushes on edge of grassy flats"
29 June 1939	UMMZ	83626	Prince Edward Dist., Emma Lake	F. Banfield (#242)	"grassy flats on edge of spruce woods"
1 July 1939	UMMZ	83627	Prince Edward Dist., Emma Lake	F. Banfield (#253)	"forest edge on grassy flats"
6 July 1939	UMMZ	83628	Prince Edward Dist., Emma Lake	F. Banfield (#272)	"bushes on edge of grassy flats"

on predators that affect duck production were in Saskatchewan. Specifically, they found *S. franklinii* at 9 of 10 sites in Saskatchewan from 1983–1985 at localities near Ceylon, Craik, Earl Grey, Goodwater, Hanley, Inchkeith, Leask, Shamrock, and Yorkton (Sargeant *et al.* 1993 and Table 3). The two sites in Saskatchewan where *S. franklinii* was most prevalent included Earl Grey and Hanley; the Earl Grey study site was the only locality in the entire study where *S. franklinii* was ranked as "numerous" (Sargeant *et al.* 1993 and Table 3).

United States

Bailey (1893) provided one of the earliest accounts of *S. franklinii* specific to the U.S. He declared, "Franklin's Spermophile is characteristic of prairies and open country, is never found in heavy timber, and does not climb trees. The places usually selected for their holes are among tall grass, weeds, and scattered brush. Often they are found living along the edge of timber that adjoins the prairie or in small groves" (p. 51). Notes on the local abundance of *S. franklinii*, provided by Bailey (1893), are included in the accounts that follow.

Illinois. The earliest account of *S. franklinii* from Illinois (Fig. 2) that I found was R. Kennicott's catalog of the animals of Cook County (Kennicott 1855). In that brief publication Kennicott said the following about *S. franklinii*: "Common. Gregarious, migratory. Found on the prairies throughout the state" (p. 579). Two years later, Kennicott published a more complete account of the mammals of Illinois in what has become a well-known work, "The Quadrupeds of Illinois, Injurious and Beneficial to the Farmer" (Kennicott 1857). In that publication, Kennicott said of *S. franklinii*, "It is far less numerous here than the striped spermophile, and appears to be a less abundant species wherever the two exist. It is observed to inhabit the thickets of low bushes, and the edges of the timber, more than the other, but does not occur in the woods" (p. 648). He provided one of the earliest accounts of variation in local abundance of *S. franklinii* when he stated, "In several instances, a company of a dozen or more have been observed to appear in a locality where none were seen the previous summer, and then to disappear after remaining there a year, or only a few weeks" (p. 648). The relationship between *S. franklinii* and the human inhabitants of Illinois as illustrated by Kennicott (1857) may hint at one factor responsible for the unpredictable nature of the species' local abundance. Apparently, *S. franklinii* often was considered an agricultural pest because it consumed newly planted corn and occasionally fed on poultry, either as eggs or chicks (Kennicott 1857). On one farm where *S. franklinii* was considered the guilty party, "a war of extermination was commenced. Several were shot, while others were killed with clubs, whereupon the survivors left, in a body, as suddenly as they had come, and were never seen again, nor could they be found upon any part of the farm" (p. 649). At least in parts of Illinois, the "wars of extermination" were successful. In 1892, G. Coleman (*in lit*, NMNH, Box 55, Folder 1) recounted, "An old farmer told me that fourteen years ago the gray and striped gophers were very numerous…but that they were now nearly all gone. He had not seen one this year."

By 1910, accounts of *S. franklinii* in Illinois mentioned their close association with agricultural land. Wood (1910) relayed, "At present a necessary condition for their habitation seems to be the presence of some shelter, such as may be furnished by tall grass, or a field of clover, alfalfa, or grain" (p. 529). This statement reflects on the adaptability of *S. franklinii* as well as the changing landscape of Illinois. Wood (1910) ranked the habitats where *S. franklinii* occurred in Champaign County from greatest to least abundance as follows: moraine bluff, till plain, and cleared pasture. Interestingly, he did not list *S. franklinii* from his "wooded bluffs" or "groves" categories although he stated, "…I presume that they may be found in the borders of woodlands" (p. 530).

Cory (1912) added little new information about *S. franklinii* in Illinois inasmuch as his account of the species was extracted primarily from Kennicott (1857). He provided the following summary of *S. franklinii*'s distribution: "In Illinois it is found in scattered communities throughout the greater portion of the central and northern portion of the state" (Cory 1912, p. 145, 147). Mohr (1943) mapped the distribution of every ground squirrel he observed between 1931 and 1942 for the Illinois Natural History Survey and found *S. franklinii* limited to the northern two-thirds of the state. In this area Mohr stated, "…I have observed Franklin's ground squirrels at almost as many

localities as woodchucks and have seen striped ground squirrels [*S. tridecemlineatus*] at two or three times as many localities" (p. 177). Anderson (1951) detailed *S. franklinii*'s presence in Fulton County in west-central Illinois as follows: "...[it] probably occurred throughout the county in prairie areas along railroads, highways, and in overgrown pastures" (p. 175). Anderson (1951) caught both *S. franklinii* and *S. tridecemlineatus* at her three trapping localities. Hoffmeister and Mohr (1957, p.139) called *S. franklinii* "common" in the northern two-thirds of Illinois in what was originally the prairie region. Their brief account stated that *S. franklinii* was found in areas of tall, thick grass with more brush than those areas frequented by *S. tridecemlineatus* (Hoffmeister and Mohr 1957).

In the spring of 1954, many species of wildlife were affected deleteriously when dieldrin, a highly toxic chlorinated hydrocarbon insecticide, was employed against a local infestation of Japanese beetles, *Popillia japonica*, in the area of Sheldon, Illinois, along the Indiana border (Scott *et al.* 1959). According to Scott *et al.* (1959, p.417), both *S. tridecemlineatus* and *S. franklinii*, which had been common in the area, suffered "virtually annihilative losses" in the wake of the insecticide application. Scott *et al.* (1959) reported that "some farmers expressed satisfaction that the dieldrin had freed their lands of ground squirrels" (p. 417). This account clearly indicated the potential negative effects that pesticide applications may have had on *S. franklinii* populations throughout much of their geographic range—where agricultural lands dominate—before the advent of stricter regulations concerning the use of these toxic chemicals.

Gray (1972) studied *S. franklinii* at the Illinois State University farm located near Normal, Illinois, in 1971 and 1972. He indicated that, in McLean County, *S. franklinii* was found mostly in hay fields and on embankments along railroad rights-of-way. In the early 1970s, McLean County was intensively farmed; idle land was limited to streambanks, roadsides, railroads, and small woodlands along streams (Gray 1972).

Van Petten and Schramm (1972) were the first researchers to strongly tie *S. franklinii* to tallgrass prairie habitat in Illinois. In their paper's introduction, they mentioned that *S. franklinii* inhabited tall grassy areas and immediately followed that comment with, "This tall grass habitat preference suggests that it [*S. franklinii*] is a climax species of the tall grass prairie" (Van Petten and Schramm 1972, p. 166). They linked perceived declines of *S. franklinii* to prairie habitats when they stated "over much of the Midwest it is absent because of destruction of suitable habitat by mowing, grazing, and cultivation" (Van Petten and Schramm 1972, p. 166). Their study detailed the introduction of a transplanted population of *S. franklinii* at the Knox College Biological Field Station. Further studies on this introduced population resulted in publications that reiterated that *S. franklinii* preferred tallgrass prairie habitat (Krohne *et al.* 1973, Krohne and Schramm 1992).

Like the efforts by those at the Knox College Biological Field Station to establish a population of *S. franklinii* on the station's restored prairie, others introduced *S. franklinii* to Gensburg Markham Prairie located near a south-Chicago suburb (Panzer and Schipp 1986). This introduction was in response to concerns that the species was disappearing from the surrounding environments. Clearly, conservation concern existed for populations of *S. franklinii* in Illinois as early as the 1970s and 1980s. Because *S. franklinii* became strongly linked to tallgrass prairie habitat at this time, the disappearance of the prairie and the squirrel became linked.

Spurred on by reported population declines in *S. franklinii*, Lewis and Rongstad (1992) examined changes in the distribution of the species in Illinois and Wisconsin. They gathered reports of *S. franklinii* from 22 locations in 16 counties in Illinois in 1985 and 1986 and concluded that it had a "relatively stable range in Wisconsin and Illinois" (p. 60). Although they did not document a decline, and in fact stated that precise data to do so were lacking, they reported that many of their sources (from mail surveys) perceived a decline. Lewis and Rongstad (1992) speculated on possible reasons for the purported decline which included: 1) *S. franklinii* may never have been common in certain regions of Wisconsin and Illinois, 2) negative effects of changes in land-use, and 3) deleterious effects associated with isolation of fragmented populations.

Hoffmeister (1989) summarized the biology of *S. franklinii* in Illinois but provided little new information. He made no mention of the species abundance or rarity within the state but said

it preferred grasses of intermediate height.

In 1998 Joyce Hoffmann, a mammalogist for the Illinois Natural History Survey, searched for *S. franklinii* at 12 sites in east-central Illinois (9 sites in Champaign County and 3 sites in adjacent Vermilion and Piatt counties) to establish the current status of the species in the state (Hoffmann 1999). She trapped known localities of historic occurrence of the species. In 1,032 trap-days she captured only one adult male *S. franklinii* along an abandoned railroad right-of-way (Hoffmann 1999).

In a related endeavor, Martin *et al.* (2003) conducted a mail survey of 166 wildlife professionals in Illinois with the objective of assessing the status of *S. franklinii* throughout its historic range. Nine extant populations were reported in the mail survey, in addition to 44 possible populations (based on unconfirmed sightings). Mail survey results, coupled with historic records and current habitat, were used to select 26 sites for live-trapping surveys of *S. franklinii*. Martin *et al.* (2003) confirmed the presence of *S. franklinii* at only three trapping sites. One population occurred in Champaign County at a restored prairie and two populations, separated by only 3 km, occurred on the same railroad right-of-way in Vermilion County, on the Indiana border (Martin *et al.* 2003). Based on these results, Martin *et al.* (2003) concluded that *S. franklinii* has declined in Illinois, but they refrained speculation on the magnitude of the decline because of the inherent difficulties in surveying for this animal.

Pergams and Nyberg (2001) concluded *S. franklinii* had declined in the Chicago region based on the rate of museum specimen deposits, and linked the decline to loss of prairie habitat in the area. Based on their data and other recent data presented here, Pergams and Nyberg (2001) suggested that *S. franklinii* be placed on the Illinois list of Threatened and Endangered Species and, in February 2004, *S. franklinii* was listed as Threatened in Illinois (*in writ.*, Illinois Endangered Species Protection Board 2004).

Recent publications by Martin and Heske (2004, 2005), both based on the *S. franklinii* population found by Martin in Champaign County, contribute further to understanding *S. franklinii* in Illinois. In one study focused on *S. franklinii* burrow placement, the authors found that more than one-third of burrow systems were "within 5 m of trees, trash heaps and buildings, whereas this habitat comprised only 9.5% of the study area" (Martin and Heske 2004, p. 229). Burrow systems also occurred disproportionately in drained soils covered by cool season grasses (Martin and Heske 2004). The authors noted that cool season grasses afford cover, forage, and nesting material at the time when the squirrels are emerging from hibernation.

In Martin and Heske (2005) a valuable glimpse into juvenile dispersal behavior in *S. franklinii* is provided. The authors reported the following: males dispersed further than females, both sexes may disperse over 1 km, agricultural fields with cover in the form of row crops may not be a hindrance to dispersal, but there is indication that for some individual *S. franklinii* roadways may serve as barriers. The authors suggest that further research on dispersal in *S. franklinii* is needed to inform management decisions concerning the species.

Indiana. The distribution of *S. franklinii* reaches its eastern limit in the northwestern corner of Indiana (Fig. 2). The earliest definitive record of *S. franklinii* in the state was in 1884, but the earliest reference may have been in 1819, as reported by Mumford and Whitaker (1982), who provided a detailed chronology of *S. franklinii* in Indiana. Bailey (1893) reported this squirrel from only two localities, both at the western edge of the state—Kentland and Earl Park. Hahn (1909) speculated that *S. franklinii* probably did not occur in more than five or six counties in Indiana. At Mount Ayr, Hahn (1909) found them "living about a stone pile in a field of oats" (p. 478). It was the only colony in the area. He commented further, "The animals were not afraid of traps and three were caught in a single trap, without bait, in two days" (Hahn 1909, p. 479).

M.W. Lyon, Jr. (1932) detailed the status of *S. franklinii* in Indiana in one of the earliest articles devoted solely to the species from any locality. Lyon (1932) believed that *S. franklinii* originally was limited to the prairie portion of Indiana because of its terrestrial nature but "with the clearing off of the timber and rendering much of the state an artificial prairie it...spread a few miles to the eastward" (p. 16). Lyon (1932) claimed that *S. franklinii* was "comparatively rare in Indiana" (p. 17). Probably for that reason he detailed all the animals he observed or that were reported to him within the state from 1930 to 1932. On 25 August

1930 he encountered a badly smashed and decomposing *S. franklinii* on a road in Pulaski County (Lyon 1932). That record may be the first account of a road-killed *S. franklinii*.

In his *Mammals of Indiana*, Lyon (1936) added little new information to his preceding account of *S. franklinii*. He reiterated their rarity in the state emphasized by his comments that "in counties where they are known to occur, it is often difficult to find persons who are familiar with them" (p. 186) and "on about three occasions have I seen it running across a road...while the Thirteen-Striped Ground-Squirrel is seen running across roads everywhere" (p. 187). He found the squirrels only in open fields and meadows.

Kirkpatrick and Conaway (1948) reported *S. franklinii* from new localities in Indiana, including a reputed colony along a railroad embankment located between Battle Ground and Ash Grove in Tippecanoe County. They speculated that *S. franklinii* seemed to have a preference for habitat provided by railroad fills (Kirkpatrick and Conaway 1948). Mumford (1969) summarized current records of *S. franklinii* in Indiana and restated the species' preference for habitat along railways. Whether that statement was based on personal observation or the previous account of Kirkpatrick and Conway (1948) is not certain. He reported the status of the species as uncommon to rare (Mumford 1969).

Mumford and Whitaker (1982) thoroughly reviewed the status of *S. franklinii* in Indiana. They reported *S. franklinii* from 16 contiguous counties in the northwest corner of the state, having observed the squirrel from 13 of those counties themselves (Mumford and Whitaker 1982). Like Lyon (1932, 1936), they found it difficult to find persons who had seen the squirrel or were at all familiar with it (Mumford and Whitaker 1982). Most observations of *S. franklinii* in Indiana occurred along roadsides or railroad embankments where the habitat was characterized by tall grass, weeds, and occasionally the presence of shrubs and small trees (Mumford and Whitaker 1982). They noted that, despite the presence of favorable habitat, *S. franklinii* had not expanded its range in Indiana to the degree that *S. tridecemlineatus* had.

In 1984, the Indiana Department of Natural Resources (DNR) listed *S. franklinii* as a species of "special concern" because of its limited distribution in the state (*in* Johnson and Choromanski-Norris 1992). That same year, the Indiana DNR began to assess the current distribution of *S. franklinii* in Indiana relative to its historic range in the state (Johnson and Choromanski-Norris 1992). The study, which occurred from 1984–1990, reported 120 individual *S. franklinii* captured from 370 surveyed sites, 139 total *S. franklinii* captures (including recaptures) in 5,161 trap days, and *S. franklinii* found at only 9.7% of sites surveyed in 9 of 16 historically occupied counties (Johnson and Choromanski-Norris 1992). Most captured squirrels (96/120) were found at railroad right-of-ways that comprised 80% of all survey sites (Johnson and Choromanski-Norris 1992). Johnson and Choromanski-Norris (1992) suggested that cooperative efforts between state agencies to manage right-of-ways for grassland habitat, and potential reintroductions of squirrels on state managed lands, might help the recovery of *S. franklinii* populations in Indiana.

Benjamin (1991) initiated a study of *S. franklinii* focused primarily on its habitat use in Indiana. He offered the following conclusions: "This study...showed that this species is not dependent on native prairie" (p. 48), and "This and previous studies suggest that vegetation characteristics alone do not determine habitat selection by *S. franklinii*" (p. 47). As a result of the preceding studies, *S. franklinii* was listed as "state endangered" in Indiana in 1990 (S. Johnson, Indiana DNR, *pers. comm.*).

In the summer of 1994, Lotter (1994) resurveyed 36 sites where S. *franklinii* had occurred according to Johnson and Choromanski-Norris (1992). She captured 29 *S. franklinii* in 1,635 trap days at 8 of 36 sites in 3 of 9 counties surveyed (Lotter 1994). She concluded that the geographic range of *S. franklinii* in Indiana had been "substantially" reduced due in part to dramatic habitat alteration of some sites (Lotter 1994, p. 7). One site was occupied by a new subdivision and another, at a railroad right-of-way, was severely disturbed when tracks were removed (Lotter 1994). In her words, the "reduction in range is most likely due to the loss of suitable habitat, due to changing farming practices and development of the northwest corner of the state" (Lotter 1994, p. 7).

Iowa. The earliest account of *S. franklinii* in Iowa that I found came from J.A. Allen (1871), who worked in the state in 1867. At that time he found the species "abundant" and noted that

"when very numerous they sometimes destroy acres of newly planted corn by eating the seed" (Allen 1871, p. 189–90). He continued, "During the spring months it is generally numerous, but after about the first of June is rarely observed, and all my efforts to obtain specimens, both in this state and in Illinois, where it is equally common, were ineffectual" (Allen 1871, p. 190).

In Council Bluffs in 1892, George Coleman (*in lit.* NMNH, Box 55, Folder 37) reported, "Both the striped and gray [*Spermophilus*] were here a few years ago but the boys have caught them all. At least none have been seen lately." In contrast, Van Hyning and Pellet (1910) said they were common throughout the state. In a similar vain Ruthven and Wood (1912, p. 204) stated, "The species is less common than *C. tridecemlineatus* but is far from rare." Spurrell (1917, p. 283) observed: "It is now common in clover and timothy fields; and when the hay is cut it removes to the grain fields and digs new burrows. It is very rarely found in pastures... this species was not as common in early days as it is now."

In *The Rodents of Iowa* Stoner (1918) provided the most detailed, historic account of *S. franklinii* in Iowa.

> "Franklin's spermophile is an inhabitant of open prairies and is not found in timbered regions, although it often lives along the edges of timber and small groves. At Lake Okoboji it is quite common near the sparse woods and groves bordering the water, and has even taken up its abode near the buildings of the Lakeside Laboratory. In most places it is not as common as the striped spermophile although in a few localities it is reported as more common than that species (p. 36–37)...This species is more migratory in its habits than the striped spermophile; the males live a wandering life during the summer, and indeed pairs or even small companies of individuals frequently migrate from one locality to another; sometimes a pair will migrate from the wintering burrow to a breeding burrow and perhaps winter in still another. This migratory habit may account for the reports received from various places to the effect that 'this species was common here last summer, but I have seen only a very few this year (p. 37).'...Although this form is quite generally distributed throughout the state, in the driftless region of northeastern Iowa it is not commonly met with. It seems, however, to be working its way into this region from the north and west, and a few miles west of the hilly section it is fairly common. At Corning it is reported that this species did not appear until 1909; now it is abundant in that locality. In almost every locality visited Franklin's spermophile is found; but its numbers are, in general, less than those of the striped spermophile (p. 37–38)...Franklin's spermophiles have long been recognized as enemies of agricultural interests and the expedient of offering bounty has been resorted to in various counties in the hope of either exterminating them or materially reducing their numbers. These sporadic attempts have not met with any degree of success. Although it is apparent that this species is recognized as more destructive in its habits than the striped spermophile, the added incentive to its capture in the way of a larger bounty offered has proved of no avail" (p. 39).

Information about *S. franklinii* in Iowa during the middle part of the 20th century is rare. Gabrielson (1921) stated the species was common in Marshall County, and Scott (1937) indicated it was found statewide after having spread into areas opened by agriculture. Both Errington (1937) and Snead and Hendrickson (1942) found *S. franklinii* remains in badger scats from Iowa. Polder (1965) thought *S. franklinii* probably was present in every county in Iowa in "favored habitats such as

hay fields, oats fields, weedy fence rows and native prairie" (p. 202). He speculated further that the "...border zone between low wet soils formed under *Spartina* and soils formed under *Andropogon* appears to be the optimum habitat both on native prairie and on cultivated lands" (Polder 1965, p. 202), but provided no support for this statement.

Bowles (1975) reported that *S. franklinii* was found locally throughout the state. Accordingly, he stated: "Prior to the settlement of Iowa, the Franklin's ground squirrel was common only in the tall-grass prairie of the central and western parts of the state. Clearing of forested areas in southern Iowa and the planting of hay crops undoubtedly increased available habitat" (Bowles 1975, p. 65). More recently Bowles (1981) listed *S. franklinii* as a mammal species declining in Iowa and attributed the decline to loss of significant areas of tallgrass prairie habitat.

Kansas. The southwestern limit of *S. franklinii*'s distribution is reached in Kansas (Fig. 2) where the squirrel is uncommon and, when present, most often is associated with brushy, grassland areas (Table 6). In the earliest reports of *S. franklinii* in Kansas, the squirrel's impacts on agriculture were the focus. A portion of a letter by L. L. Dyche, biology professor at the University of Kansas, sent to Vernon Bailey in 1888 stated: "Not much damage is done by this species...except in certain localities...The squirrels dig up the corn (and sometimes other seeds) soon after it is planted in the spring and in the fall do some damage by burrowing under corn shocks...We killed many of them with guns and tried to poison them, with apparently very little success" (Bailey 1893, p. 52–3).

Remington Kellogg (1915) prepared his Master's thesis on the mammals of Kansas and provided a detailed account of *S. franklinii*. Unfortunately it is not clear how much of that account was based on observations from Kansas. Whereas Kellogg (1915) examined only four *S. franklinii* specimens from Kansas, he frequently observed the species in North Dakota in the summer that preceded the writing of his thesis (see Table 8). Nevertheless, his comments provide an historic insight that warrants repeating here. He found that *S. franklinii* "is not common in the open prairie country as it depends on the cover of brush and timber" (Kellogg 1915, p. 162) and reinforced Dyche's earlier observations with the following comments: "Franklin's spermophile is exceedingly destructive to corn. They dig up the corn after it is planted in the spring and eat out the kernel. This frequently necessitates replanting. In some localities their depredations are so destructive that the farmers sow the fields with poisoned corn before planting" (Kellogg 1915, p. 163).

In contrast to the abbreviated commentary most authors afforded *S. franklinii* in Kansas, Andersen and Fleharty (1967) provided specific details on the habitat associations of a *S. franklinii* population they located in northeastern Jewell County in 1964. The habitat was dominated by smooth brome (*Bromus inermis*) over two feet in height, but also contained Maxmillian sunflower (*Helianthus maximilianii*), Indian hemp (*Apocynum cannabinum*), smartweed (*Polygonum* spp.), stinging nettle (*Urtica dioica*), and smooth sumac (*Rhus glabra*). Along one edge of the area were several wild plum (*Prunus* sp.) thickets (Andersen and Fleharty 1967). They collected two squirrels, and found seeds of smartweed, wild plum, and beetle remains in their stomach contents. An opened cache of wild plums was located near one of the burrows (Andersen and Fleharty 1967).

By 1973, Platt *et al.* (1973) listed *S. franklinii* as rare in Kansas and indicated that isolated populations occurred in relict areas of tallgrass prairie. In an effort to supplement the squirrel's habitat needs, the authors tried to encourage landowners to leave a swath of native grass around plowed fields. They also encouraged the highway department to permit native prairie cover to develop along roadsides and to minimize mowing (Platt *et al.* 1973).

Minnesota. Vernon Bailey, active in the formative years of the U.S. Biological Survey, provided many of the earliest accounts of *S. franklinii*. He first observed the species at Elk River, Minnesota, in 1872 (Bailey 1893). They

were scarce at that location, and he saw only 6 to 8 individuals a year for the 14 summers he lived there (Bailey 1893). Notes on *S. franklinii* from Bailey and others employed by the U.S. Biological Survey are in Table 7. At other localities in Minnesota, *S. franklinii* was more common. At Ortonville in Big Stone County in 1887, they were abundant and Bailey (1888, p. 438) wrote, "A few are scattered over the prairie, but in the timber near the lake, and in the ravines, there are a great many…On the prairies they are mostly found near grain-fields or in marshy places." In the same year at Brown's Valley in Traverse County, he wrote, "Occasionally found on the prairie, and very numerous all over the valley, even in town" (Bailey 1888, p. 439).

As early as 1892, Herrick (1892) recognized declining populations of *S. franklinii* in southern Minnesota. He stated, "This graceful animal was at one time fairly abundant throughout the southern part of Minnesota, but is being rapidly exterminated by civilization" (p. 167). He added, "It is still abundant about Big Stone Lake [on the western border of Minnesota near the North Dakota / South Dakota border], where it will approach the traveler's tent fearlessly and may be taken by the hand if desired" (Herrick 1892, p. 167). Herrick (1892) said that *S. franklinii* is found "about the edges of copses and it is not unusual for the animal to take refuge in a low tree or close thicket rather than its burrow" (p. 167).

The carnivorous tendencies of *S. franklinii* were first noted by A.M. Johnson (1922), who relayed his account of an attack on a rabbit in a "vacant yard in the forest of western Aitkin County" (p. 187) in Minnesota. C.E. Johnson (1930), writing of his experiences in northwestern Minnesota during the years 1889–1902, recalled of *S. franklinii*, "On our homestead it was of rather common occurrence along the banks of the coulee and along the margins of the fields, where tall weeds, grass or scattered shrubbery formed suitable habitats" (p. 445).

Fifty years after Herrick (1892) noted declining populations of *S. franklinii* in southern Minnesota, Swanson *et al.* (1945) declared the following: "The Franklin ground squirrel is no longer a common species in the southern part of the state, but in the northwestern counties it is quite abundant. In 1932 I found it as common as the striped species in Lake of the Woods and Roseau counties" (p. 77–8). Swanson *et al.* (1945) considered Lake of the Woods and Roseau counties, both found along the Canadian border, to be boreal habitat.

Gunderson and Beer (1953) summarized accounts of *S. franklinii* in Minnesota and mapped sites of its verified occurrence in the state. Of its habitat associations, they stated "It prefers brushy fields, and in Minnesota is often found in rock piles at the edges of woods" (Gunderson and Beer 1953, p. 77).

The long-term presence of *S. franklinii* at the University of Minnesota's Field Station at Itasca State Park in north-central Minnesota, which lies within the coniferous forest zone, has resulted in three publications involving the squirrels. Orr (1958) conducted a short-term behavioral study of *S. franklinii* at the field station, Haggerty (1968) conducted one of the first ecological studies devoted to *S. franklinii*, and Erlien and Tester (1984) analyzed population dynamics of all squirrels in the park. The results of Orr (1958) add little to the discussion here, but results from Haggerty (1968) and Erlien and Tester (1984) deserve further mention.

Haggerty (1968) observed *S. franklinii* in and near picnic areas and campgrounds within Itasca State Park and at the field station's property. Mowed areas with scattered clumps of trees, shrubs, and tall herbaceous vegetation characterized these areas (Haggerty 1968). She indicated that *S. franklinii* utilized mowed areas only when in proximity to brush or areas of tall grass. Based on trapping efforts during 1954–1966 by her and students in a vertebrate ecology class taught at the field station, 193 individual *S. franklinii* were captured, including 63 adults and 130 juveniles. An additional 66 squirrels were captured from three years of intermittent trapping at picnic grounds within the park (Haggerty 1968). Haggerty (1968) documented population fluctuations in *S.*

Continued on page 24

Table 6. Notes on Franklin's ground squirrel, *Spermophilus franklinii*, in Kansas.

Locality	Habitat	Abundance	Citation
Kansas		"Not common" (p. 22).	Knox 1875
Kansas		"Found in most parts of the state; not common" (p. 173).	Lantz 1905
Geary County, along the Missiouri River	"small pastures and fields on the upland back of the bluffs" (p. 143).		Linsdale 1928
Kansas	"prefer denser cover than the other Kansas species, and are usually found in bushy or grassy border lands" (p. 176).	"extremely rare along periphery of the range; not common anywhere in Kansas" (p. 176).	Black 1937
Leavenworth County, Fort Leavenworth Military Reservation	Missouri River bank. buckbrush-sumac association.		Brumwell 1951
Kansas	"They prefer denser cover than the other Kansas ground squirrels, and are usually found in the brushy or grassy fence rows and in pasture lands" (p. 128).		Cockrum 1952
Lyon County		"Scarce" (p. 190). "Fisherman and other sportsmen frequently report seeing 'large ground squirrels' in the park [Lyon County State Park]" (p. 190).	Clarke et al. 1958
Kansas	"makes its home where the vegetation is so high that the animal cannot see over it and so dense that the animal cannot see through the vegetation for more than a few feet" (p. 95).	"One that my dog caught one and a half miles south of Le Loup, Franklin County, was the only one seen in the seven years that I lived there" (p. 95).	Hall 1955
Kansas	"the zone where tall grass prairie and deciduous forest come into contact. It prefers the sheltered cover of dense grasses, weedy fields and wastelands, and shrubby forest edges" (p. 91).	Uncommon (part of this is due to its wary nature).	Bee et al. 1981

Table 7. Accounts of Franklin's ground squirrel, *Spermophilus franklinii*, in Minnesota from notes recorded by U.S. Biological Survey personnel contained in the archives at the NMNH.

Locality	Habitat	Abundance	Source
Moorhead, Clay County		"This animal is seen here occasionally, but not in any great numbers."	O.J. Murie 1919 Box 62, Folder 24
Minnesota	"I found it fairly common"	"in the heavy woods on the Chippewa, where it seemed especially fond of Norway pine areas with an under-growth of hardwoods."	O.L. Augstin, Jr. 1930 Box 61, Folder 21
Itasca Lake, Clearwater County	"They occasionally run across the road but generally keep under cover of weeds and brush and close to through their burrows."	"These big gray ground squirrels with bushy tails & minute ears are found through this region but are rarely seen."	V. Bailey 1932 Box 62, Folder 6
Red Lake		"A Franklin's ground squirrel was seen crossing the road near the Ranger Station at Washkish."	V. Bailey 1932 Box 62, Folder 6

Table 8. Accounts of Franklin's ground squirrel, *Spermophilus franklinii*, in Nebraska from notes recorded by U.S. Biological Survey personnel contained in the archives at the NMNH.

Locality	Habitat	Abundance	Source
Ames, Dodge County	"This specimen was the only one I saw in two days over the prairie."	"I shot one gray spermophile in a stubble field about 3/4 mile N.E. of Ames. The owner of the land told me they were quite plenty [sic] and took up consider-able young corn in the spring."	G. Coleman 1892 Box 68, Folder 32
Columbus, Platte County	"4 were caught in small steel traps. No. 198 was caught at [a] hole in prairie land. No. 211 at [a] hole in [an] oat field. The other two were caught in traps set for *Geomys*. I saw several more running on prairie and in stubble fields."		G. Coleman 1892 Box 68, Folder 32
Kearney, Buffalo County		"2 of the gray species were caught—one preserved...Buffalo Co. gives a premium of 3 cents each for [something?]. The boys keep them pretty well killed off near town."	G. Coleman 1892 Box 68, Folder 32
Knox County		"common at Niobrara where a female killed June 9 contained 7 small embryos. They were said to occur at Verdigre, Knox Co."	V. Bailey 1893 Box 68, Folder 14
Cuming and Holt counties		"one seen from the car window [train car] between Beemer and Wisner. At Ewing a boy described them and said he had killed 2, but they were very scarce."	V. Bailey 1894 Box 68, Folder 15
Knox County	"At Verdigris living in holes in the sides of ravines, and at the bases of hills bordering the valley."	"Appears to be abundant. Farmers say it is very destructive to growing corn."	M. Cary 1903 Box 68, Folder 23
Halsey, Thomas County		"Gray ground squirrels are not very common. Near Russell one of the station employees saw one July 10."	D.E. Lautz 1910 Box 68, Folder 37

franklinii, indicated by the following densities: 0.09 *S. franklinii*/ha in 1954, 0.04/ha in 1958, 0.24/ha in 1960 and 1961, 0.09/ha in 1963, and 0.08/ha in 1964.

Haggerty (1968) noted *S. franklinii* dispersal throughout the active season, but particularly in May and late summer. Those *S. franklinii* with the greatest tendency to travel long distances included juveniles, spring yearlings, and males, in contrast to adults in general and females in particular (Haggerty 1968). Maximum documented movements of presumed dispersers were 0.8–1.6 km. Some adult males moved as much as 152–304 m in a few hours (Haggerty 1968). Low survivorship in *S. franklinii* complicated efforts to gather more detailed information on dispersal. Only 11 of 130 juveniles were recaptured as yearlings, indicating a high rate of mortality and/or emigration during the first year of life (Haggerty 1968). Similarly, maximum known ages of adults were 5 and 2 years, for females and males respectively (Haggerty 1968).

Erlien and Tester (1984) analyzed *S. franklinii* capture rates at Itasca State Park for 1954–1975, incorporating data collected by Haggerty (1968), and reported a periodicity of 10–11 years for population peaks. The cyclic pattern of *S. franklinii* populations was the strongest of the squirrels tested (r^2 of 0.81 in serial correlation analysis). They speculated that the cyclic patterns of *S. franklinii* might be the result of prey-switching by predators of snowshoe hare (*L. americanus*) and ruffed grouse (*Bonasa umbellus*). Population peaks and valleys of *S. franklinii* lagged behind those of both *L. americanus* and *B. umbellus* for the same period (Erlien and Tester 1984).

Accounts of *S. franklinii* in Minnesota from the last quarter of the 20th Century further detail its presence in the primarily wooded portions of the northern part of the state. Robins (1970–1971, p. 31) found *S. franklinii* "numerous in the mid-1960s in several public campgrounds on the west side of Lake Winnibigoshish and around Cut-Foot Sioux Lake in Itasca County" in north-central Minnesota. He also reported *S. franklinii* from the Duluth area, in northeastern Minnesota, which previously had fallen outside the geographic range of the species (Robins 1970–1971). Robins (1970–1971) found *S. franklinii* in brushy fields or near the edges of woods. Hazard (1982, p. 63) declared that *S. franklinii* "prefers brushy and partly wooded areas, as well as prairie edges, rather than open prairie" and that this habitat preference, plus a tolerance for people, explains its common occurrence in campsites, state parks, and open dumps. Hazard (1982) updated the distribution of *S. franklinii* in Minnesota and remarked that the species "has moved north and east into the forest biomes as land has been cleared" (p. 63).

Lewis (1988) examined population structure and reproductive characteristics of *S. franklinii* from animals trapped from the Mid-continent Waterfowl Project in Ottertail, Grant, and Douglas counties in west-central Minnesota. Based on trapping success (measured in trap-nights per squirrel), *S. franklinii* populations increased in those areas from 1984–1987 as follows: 53 squirrels trapped in 1984, 60 in 1985, 118 in 1986, and 155 in 1987 (Lewis 1988). The study area was predominately agricultural (corn, oats, and wheat, primarily), with Waterfowl Production Areas in the area consisting principally of prairie and wetland habitat (Lewis 1988).

Sargeant *et al.* (1993) reported *S. franklinii* from all three of their study sites within Minnesota (Table 3). Oak trees were common in woodlots at all three sites and at those near Hawley and Hitterdal, they ranged up to 0.65 km^2. The authors ranked the presence of *S. franklinii* at their Minnesota study sites as either "scarce" or "uncommon" (Sargeant *et al.* 1993 and see Table 3).

Missouri. I located little information on *S. franklinii* specific to Missouri. Coues and Allen (1877) wrote that the geographic range of *S. franklinii* extended from northern Missouri to the Great Slave Lake in the Northwest Territories of Canada. Although the species does not occur as far north as the Great Slave Lake (one of several geographical inaccuracies in Coues and Allen's account), its geographic range in Missouri is limited to the northern part of the state (Fig. 2).

Schwartz and Schwartz (1981) provided an excellent account of the natural history

of *S. franklinii*, but it is difficult to ascertain how much of their information is specific to Missouri. They reported it limited to the western and northern parts of the state and indicated that while it occupies the Prairie Region of Missouri "it prefers the marginal habitat afforded by fence rows, wooded banks, gullies, and little-grazed sod" (Schwartz and Schwartz 1981, p. 144).

Ellis (1982) studied a population of *S. franklinii* along a railroad right-of-way located 4 km S of Atlanta in Macon County in the north-central part of Missouri. He captured 47 individual *S. franklinii* on his study site of 2.4 ha (Ellis 1982). Only 4 of 15 adult squirrels were regularly recaptured, and he thought only 18 of 32 juveniles were born on the site (Ellis 1982). New juveniles were captured on the site from August through early October. He concluded that many *S. franklinii* captured on his site were transitory animals and that young dispersed in fall (Ellis 1982).

Ellis (1982) identified three traits of his site he felt contributed to the large population of squirrels found there: 1) considerable vegetative cover, principally in the form of grasses (primarily Japanese and smooth brome, *B. japonicus* and *B. inermis*), 2) relatively little disturbance—in contrast to areas that are grazed, hayed, or farmed, and 3) topography and substrate suitable for burrow construction. The site also contained a border of trees along a fencerow and the occasional shrub or tree along the right-of-way that Ellis also felt might be important habitat factors. He believed the lack of disturbance at the site contributed to its vegetative characteristics and the squirrel's continued presence. Unfortunately, he noted that the three habitat traits he identified rarely occurred in areas other than railroad right-of-ways in northeast Missouri (Ellis 1982). That statement may hold true for much of the lower Midwest. Nevertheless, Ellis concluded that *S. franklinii* was relatively common in northern Missouri and that the species should not be considered rare, threatened, or endangered in the state. However, he did recommend that, because of the squirrel's preference for tallgrass habitat, prairie should be conserved and restored in Missouri (Ellis 1982).

DeSanty-Combes (2001), biologist for the Missouri Department of Conservation, recently summarized 60 years (1941–2001) of distributional data for *S. franklinii* in Missouri. She recorded it from 69 localities in 27 counties, based on museum specimens, written reports, and recently reported sightings gathered from a mail-survey (DeSanty-Combes 2001). Twenty-seven of these localities were reported from 1990–2001 and 16 occurred in 2001 alone (DeSanty-Combes 2001). At nearly 80% of sites visited by her in June 2001, most shared characteristics that included "wide grassy roadside ditches or brushy fence rows (with an embankment suitable for burrowing), tree rows providing an edge component, cropland, and grassland" (DeSanty-Combes 2001, p. 1). In the course of visiting sites, DeSanty-Combes discovered one *S. franklinii* roadkill (in approximately 25 hours and 1,192 miles of driving). One additional *S. franklinii* roadkill was reported in her 2001 mail survey (DeSanty-Combes 2001). Another state biologist trapped one adult male and one juvenile female in a 30-trap-day effort in July 2001 at a site where *S. franklinii* were observed earlier in the summer, but subsequent trapping at the location (90 additional trap-days) produced no additional animals (DeSanty-Combes 2001).

DeSanty-Combes continued her survey efforts for *S. franklinii* in 2002. Another mail survey resulted in 32 more reported sightings, of which 29 were from new locations (DeSanty-Combes 2002). She visited many of these sites to verify the squirrel's presence. Because *S. franklinii* has been recorded from only 16 of 27 historically occupied counties since 1990, she proposed that further research be conducted to determine the ecological factors limiting the distribution of the species within Missouri. As a result of her recent findings, the status of *S. franklinii* in Missouri changed from S4 to S2S3, which indicates that the species is rare and may be locally imperiled (DeSanty-Combes 2002).

Nebraska. Warren (1875, p. 93) collected one *S. franklinii* "near the mouth of the Loup Fork of the Platte" where he found them "quite rare"

in his explorations during 1855–1857. In contrast, Aughey (1880, p. 120) reported *S. franklinii* as "common on the prairies" of Nebraska. Perhaps, as was true elsewhere throughout its geographic range, the abundance of *S. franklinii* in Nebraska varied locally. A portion of a letter from Lawrence Bruner (a professor at the University of Nebraska), reprinted by Bailey (1893, p. 52), supported this view: "Franklin's Spermophile is quite common in some parts and rare in others." Swenk (1908, p.30) considered *S. franklinii* locally abundant and "very common in eastern Nebraska east of the 98th meridian." First-hand accounts from U.S. Biological Survey reports (Table 8) provided more specific information about *S. franklinii* in Nebraska around the turn of the nineteenth century.

No detailed accounts from the first-half of the twentieth century address the habitat associations or local abundance of *S. franklinii* in Nebraska. Although during this time the species was of sufficient abundance and availability to serve as a study organism for Otis Wade, a professor at the University of Nebraska who published several works on hibernation in ground squirrels (Wade 1930, 1948, 1950; Wade and Gilbert 1940). Later, Jones (1964) summarized the status of *S. franklinii* in the state prior to 1960. He considered it "typically an inhabitant of the tall-grass prairie of the eastern part of the state" (p. 124) and noted that burrow sites occurred in "tall grass, brush, or the wooded borders of grassy areas" (Jones 1964, p. 125). As early as the 1960s, he perceived a decline of the squirrel in the southeastern region of Nebraska and commented, "In my own experience, Franklin's ground squirrel was seen more frequently in the vicinity of Lincoln 15 years ago, even 10 years ago, than today" (Jones 1964, p. 125).

Haberman and Fleharty (1971, p. 77) found *S. franklinii* "common in low-lying areas near bridges and along road sides and railroad right-of-ways" in Boone County. The burrows of their study population were in stands of smooth brome (*Bromus inermis*) with an abundance of chokecherry (*Prunus virginiana*) bushes and wild plum (*Prunus americana*) thickets nearby (Haberman and Fleharty 1971). According to citizens of Boone County, in 1969 populations of *S. franklinii* were at a 20-year high and now were occurring near buildings and hay bales on local farmsteads (Haberman and Fleharty 1971).

Data on *S. franklinii* in Nebraska were gleaned from two additional published sources. Pivorun and Sinnamon (1981), although they provided no specific locality, trapped 30 *S. franklinii* in Nebraska in May 1978 for their study of blood coagulation in hibernating ground squirrels. This certainly indicates the presence of a sizeable local population, or populations, of *S. franklinii* in Nebraska at that time. Manning and Geluso (1989) reported a single sight record of *S. franklinii* from about 20 km east of the Halsey National Forest property, in central Nebraska. The animal was in tall grass along the road near the Middle Loup River (Manning and Geluso 1989).

North Dakota. Elliott Coues found *S. franklinii* abundant at Pembina, North Dakota, near the Canadian border prior to 1877 (Coues and Allen 1877). Years later they were still common at Pembina, according to Bailey (1888), who found them in brush, prairie meadows, and fields. At Devil's Lake in Ramsey County, he (Bailey 1888, p. 439) observed that they seemed "to prefer woods or low marshy and weedy land." He later added that, at Devil's Lake, "they were most common in the straggling groves of small trees a little back from the lake, and many of their burrows were placed under logs and stumps or between the roots of trees" (Bailey 1893, p. 51). A few years later, A.K. Fisher of the U.S. Biological Survey observed that the population at Devil's Lake had declined (see Table 9).

In the early 1900s in parts of eastern North Dakota, *S. franklinii* frequently was considered common or abundant and usually found associated with habitat that contained a woody component (Table 9). Bailey *et al.* (1914, p. 7) stated, "They are not generally distributed over the open prairie country, but depend on the cover of brush and timber, and in suitable areas become very numerous and extremely destructive." Bailey (1926) reiterated those thoughts more than a decade later. Agricultural practices certainly caused changes in local abundance of *S. franklinii* in North Dakota. In areas where they were once uncommon, they suddenly occurred in great numbers, only later to decline to the point of disappearance—certainly due in part to attempts to exterminate them as agricultural pests (Table 9).

Since the early surveys, the literature concerning *S. franklinii* in North Dakota has dealt principally with the species as a predator of duck nests—*S. franklinii* is known to consume duck eggs (Sargeant *et al.* 1987, Choromanski-Norris *et al.* 1989, Sargeant *et al.* 1993). One of these studies—Choromanski-Norris *et al.* (1989) (based on Choromanski-Norris 1983)—resulted in the most carefully measured information on habitat use by *S. franklinii* within the state. They tracked *S. franklinii* within a waterfowl production area using radio-telemetry. In their study, conducted in Stutsman County in central North Dakota, the most intensively used portion of the study area was in, and in proximity to, a tree-belt that was composed principally of Russian olive (*Elaeagnus angustifolia*), chokecherry (*Prunus virginiana*), plum (*Prunus* spp.), red-osier dogwood (*Cornus stolonifera*), and lilac (*Syringa* spp.) (Choromanski-Norris *et al.* 1989). Because the tree-belt constituted approximately 1.5% of available habitat, its high use indicated a strong habitat preference by the squirrel (Choromanski-Norris *et al.* 1989).

Sargeant *et al.* (1993) found *S. franklinii* at seven of nine study sites in North Dakota (see Table 3). They considered it "scarce" at all locations except Sharon, where it was considered "uncommon" (Sargeant *et al.* 1993 and Table 3). All of the North Dakota study sites were included in the prairie zone of the Prairie Pothole region (Sargeant *et al.* 1993 and Table 3).

South Dakota. Four museum specimens (NMNH 14914, 21831, 192729, 192730) collected at Fort Sisseton in the northeastern part of South Dakota in 1887 comprise the earliest evidence of *S. franklinii* in the state. A few years later, in 1893, Bailey wrote that *S. franklinii* was, "Common at Scotland where one specimen was taken" and "said to be quite common at Running Water" (*in lit*, NHMH, Box 90, Folder 17). Both Scotland and Running Water are located in the southeast corner of South Dakota. Over and Churchill (1945) indicated that the range of *S. franklinii* did not extend much beyond the Missouri River and that, in the southeastern part of the state, "it frequents the highways and lives in the banks along the roadside" (p. 25). They reported that it "no doubt destroys many eggs and the young of ground nesting birds" (p. 25) and supported that statement with an account of a squirrel destroying two nests—one identified as quail, *Colinus virginianus* (Over and Churchill 1945).

Findley (1956), Choate and Jones (1981), Sargeant *et al.* (1993), and Higgins *et al.* (2000) add little more to the account of *S. franklinii* in South Dakota. Findley recorded the species from Clay County, but provided no specific information about the specimen. Choate and Jones (1981) included *S. franklinii* in their account of mammals found in the state and remarked that the western limits of its distribution were poorly known. Sargeant *et al.* (1993) recorded *S. franklinii* from near Parkston, the only one of their three South Dakota study sites where the species was observed (see Table 3). Most recently, Higgins *et al.* (2000) provided a general account of the species within the state. They stated that, although found in brushy areas or along woodland edges, the squirrel favors areas of dense grass, such as may be found in tallgrass or mixed-grass prairies (Higgens *et al.* 2000).

Wisconsin. Strong (1883) provided the earliest record of *S. franklinii* from Wisconsin that I found. He reported it from the prairie regions, noted it frequently inhabited cultivated fields and did not occur as commonly as *S. tridecemlineatus*. Bailey (1893) found the northernmost records of *S. franklinii* in Wisconsin at Plover and Ripon—in central and south-central Wisconsin, respectively. It was rare at those localities (Bailey 1893). Snyder (1902) collected three specimens in Dodge County: one near some barns in 1891; a second which was dug from its burrow in an oat field in 1892; and a third in 1900 after it was observed running along a road bordered by fields of newly sown grain and clover. Snyder (1902) received reports of the commonness of *S. franklinii* in certain townships of Dodge County, but also mentioned his own difficulties in finding the species on a consistent basis.

Jackson (1908, p. 18) considered *S. franklinii* generally "rare in all sections of the state" but noted "careful observation will prove them quite common west from Rock County to the Mississippi River and north to Pepin County." He said they occurred in fields of growing grain and along fencerows and observed that they moved to areas of tall grasses when the grain fields were cut (Jackson 1908). He felt the shyness of the species contributed to the lack of information concerning it within Wisconsin

Continued on page 31

Table 9. Accounts of Franklin's ground squirrel, *Spermophilus franklinii,* in North Dakota from notes recorded by U.S. Biological Survey personnel contained in the archives at the NMNH.

Locality	Habitat	Abundance	Source
Devils Lake, Ramsey County		"Franklin's Spermophile was apparently very rare as only one specimen was secured. A few years since Mr. Bailey found it common, but found Richardson's Spermophile very rare, which species at the present time is very abundant."	A.K. Fisher 1893 Box 79, Folder 16
Lisbon, Ransom County		"Said to be not common; I did not see any."	A.K. Fisher 1893 Box 79, Folder 16
LaMoure, LaMoure County	"In one locality the notes of a number were heard among a thick growth of *Symphoricarpos occidentalis* along the banks of the James River."	"Quite common."	A.K. Fisher 1893 Box 79, Folder 16
Grafton, Walsh County	"being found in pasture prairies chiefly."	"This Franklin's ground squirrel is also numerous at this locality."	H.V. Williams 1912 Box 80, Folder 25
Walhalla, Pembina County	"inhabiting the timber and brushy districts. They live in holes usually at the foot of a tree or stump."	"This ground squirrel is also abundant thru this locality."	H.V. Williams 1912 Box 80, Folder 25
Wales, Cavalier County	"They inhabit the prairie lands where it is level and also the grain fields, but are never found in the timber."	"The Franklin's ground squirrel is very plentiful here."	H.V. Williams 1912 Box 80, Folder 25
Birchwood, Rolette County	"living chiefly in the timber but on occasion a specimen is found out on the prairies."	"These ground squirrels are very plentiful at this locality."	H.V. Williams 1912 Box 80, Folder 25
See information in the account within the "Abundance" section in this row.		"From St. John homeward by way of Canada the country is overrun with the Franklin ground squirrel. They are the thickest near Starkweather...A decrease in numbers was noticed after reaching Adams and very few were seen from there to Park River while none from Park River to Grafton."	H.V. Williams 1912 Box 80, Folder 25
Portland, Traill County		"After reaching the delta saw no more of the Richardsons ground squirrel, its place being taken by the Franklin's and the Striped."	A. Eastgate 1912 Box 79, Folder 15

Table 9 continued

Locality	Habitat	Abundance	Source
Valley City, Barnes County	"all along the river and larger ravines where any small brush and tall weeds grow."	"common in [the] river valley."	A. Eastgate 1912 Box 79, Folder 15
Kathryne, Barnes County		"Very common along the valley and on the higher prairie."	A. Eastgate 1912 Box 79, Folder 15
Lisbon, Ransom County		"Very common all along the valley."	A. Eastgate 1912 Box 79, Folder 15
Fairmount, Richland County	"They inhabit the ground chiefly along the course of the Bois de Sioux River where they make their burrows in the nettles."	"abundant throughout the southeastern part of the state." "They are becoming a pest in this section of the state and I was told by many farmers that three years ago they did not know such an animal existed and [they] have become more numerous each year."	H.H. Sheldon 1915 Box 80, Folder 16
Lidgerwood, Richland County	"inhabiting grass bordering grain fields."	"Very abundant."	H.H. Sheldon 1915 Box 80, Folder 16
Oakes, Dickey County	"along [the] James River where the tall grass offers concealment for their burrows which in usually every case are adjacent to grain fields."	"Abundant."	H.H. Sheldon 1915 Box 80, Folder 16
Ellendale, Dickey County		"These squirrels have never been common in this vicinity...However it does occur."	H.H. Sheldon 1915 Box 80, Folder 16
Wahpeton, Richland County		"occurs in this locality."	R. Kellogg 1915 Box 80, Folder 2
Grafton, Walsh County	"several seen in hay field."		R. Kellogg 1915 Box 80, Folder 2

Continued on next page

Table 9 continued

Locality	Habitat	Abundance	Source
Drayton, Pembina County		"Does a great deal of damage to the growing corn."	R. Kellogg 1915 Box 80, Folder 2
Manvel, Grand Forks County		"Farmers here endeavor to kill these ground squirrels off as fast as they see them because of the damage they do."	R. Kellogg 1915 Box 80, Folder 2
Larimore, Grand Forks County	"Two were taken on the edge of a wheat field."		R. Kellogg 1915 Box 80, Folder 2
Tokio, Warwick, and Fort Totten, Benson County	"One can hear their whistle in the woods and on the edge of brush patches."	"Common."	R. Kellogg 1915 Box 80, Folder 2
Towner, McHenry County	"I found this ground squirrel most common in the brushy patches in the sandhills. I also saw one in the meadow near Mouse River."		R. Kellogg 1915 Box 80, Folder 2
Fargo, Cass County		"is found here, but in much smaller numbers than the last species [*S. tridecemlineatus*]."	O.J. Murie 1919 Box 80, Folder 13

Table 10. Tabulation of specific accounts of Franklin's ground squirrel, *Spermophilus franklinii*, reported in the text that address *S. franklinii* populations and habitat use. Refer to Appendix Table 1 to see the list of citations used to construct this table.

	Characterization of population(s)		Characterization of habitat			
Publication year of citation	Common, abundant, increasing, or a pest	Uncommon, rare, or declining	Fluctuating or variable in occurrence	Prairie[1]	Savanna[2]	Woodland[3]
Pre - 1950	32	18	10	16	28	2
Post - 1950	8	22	9	19	31	0
Totals	40	40	19	35	59	2

[1]=Habitat description includes no mention of woody vegetation, only grasses and forbs.
[2]=Habitat description includes mention of both grassy and woody vegetation.
[3]=Habitat description includes mention of only woody vegetation

(Jackson 1908). Hollister (1908) reiterated some of Jackson's points and added a few additional details that contribute to the picture of *S. franklinii* in Wisconsin. He found it "common in isolated colonies in various parts of Walworth County" (Hollister 1908, p. 139). The largest colonies occurred on the "Ridge Prairie" and on the border of the "Big Marsh" near Delavan. At Big Marsh he shot one out of a tamarack tree (*Larix laricina*) "from a considerable height," having mistaken it for a gray squirrel (Hollister 1908, p.139).

Schmidt (1931, p. 111) collected one *S. franklinii* that "was living in brush consisting of poplar, soft maple, and jack pine, in which there were a few open spaces grown up to sweet fern and blueberries" in western Clark County in 1927 or 1928. He examined the stomach contents of that individual and found it contained 20% "highbush blueberries", 30% "blueberries", and 50% "white roots" (Schmidt 1931, p. 111).

The most extensive information concerning *S. franklinii* in Wisconsin is from Jackson (1961). About its habitat associations, in addition to the citations already referenced, he added: " sometimes [it is found] in fairly heavy woods, particularly of Norway or jack pine, if sufficient undercover of ferns, grass, or low shrubs is present; rarely in the vicinity of barns or farm houses" (Jackson 1961, p. 140). He considered the "sheltering cover of tall grass or other herbage...a necessary condition for its habitat" and noted "it is not found in closely grazed or mowed pastures, fields, lawns, or cemeteries where the striped ground squirrel might be common" (Jackson 1961, p. 140). Jackson (1961) said the species could not be considered common in Wisconsin, but added that it is probably more "plentiful than records indicate" (p. 140). Like many others, he commented on the variable nature of *S. franklinii* populations when he stated, "It may become common at times in isolated small colonies, but tends to shift its homesite and may be present one day, gone the next, and back again in a few weeks, another year, or several years" (Jackson 1961, p. 140).

Lewis and Rongstad (1992) gathered reports of 35 sightings of *S. franklinii* from 28 locations in 14 Wisconsin counties in 1985 and 1986. Reports revealed concentrations of squirrels in Douglas, Burnett, and Rusk counties in northwest Wisconsin, and in Waukesha, Racine, and Kenosha counties in southeastern Wisconsin, as well as at scattered localities in a northwest band through the center of the state (Lewis and Rongstad 1992). In his thesis, Lewis (1988) suggested that populations of *S. franklinii* at Crex Meadows Wildlife Area in Burnett County and Bong Recreation Area in Racine County might serve as source populations for reintroductions elsewhere. However, I was unable to locate squirrels in brief searches at either Crex Meadows (visited in 1999) or at Bong (visited in both 2000 and 2001). Refuge personnel at Crex Meadows indicated that *S. franklinii* were fairly common 8–10 years ago but have not been seen regularly since then (P. Petersen, *pers. comm.*).

Anthony (1999) initiated the Wisconsin Small Mammal Survey for his M.S. thesis. The effort involved coordinating volunteers to survey various grassland habitats in southern Wisconsin to establish base-line data and habitat preferences of small mammals. Anthony (1999) recorded *S. franklinii* from only 1 of 16 study sites in 24 trapping events spanning 1995–1997. The squirrel was found in August 1997 at Chiwaukee Prairie, located in the extreme southeast corner of the state (Anthony 1999).

DISCUSSION

Several generalizations can be made about *S. franklinii* based on the preceding accounts. First, throughout its geographic range, *S. franklinii* usually occurs in habitat that contains both grassy and woody components. Of 96 specific accounts, 59 clearly indicate that both grassy and woody vegetation were present in habitat occupied by *S. franklinii* (Table 10). Second, the squirrel frequently exhibits changes in local abundance. Lastly, according to the published literature since 1950, *S. franklinii* is considered less common in general (Table 10). More specifically it is encountered less frequently in the southern portion of its geographic range than in former times. Of 22 accounts published since 1950 that indicate *S. franklinii* is uncommon, rare, or declining (Table 10), 15 of these are from the four states (Indiana, Illinois, Missouri, and Kansas) that occupy the southernmost portion of *S. franklinii's* geographic range. (Refer to Appendix Table 1 for specific information on the citations used to construct Table 10.) Each

of these generalizations will be expanded upon in the following paragraphs.

Habitat

Historical and natural associations. From the earliest accounts to the present, even prehistorically, *S. franklinii* most commonly has been found in habitat containing a mix of grassy and woody components. This mixture of vegetation occurs at the interface of many different types of woodland—both deciduous and coniferous—and grassland habitats. Woodland edges, grassy openings within woods, wooded valleys within grasslands, riparian corridors, and grasslands that include scattered trees and shrubs, all constitute habitat suitable for *S. franklinii*.

In the southern part of its geographic range, many have referred to *S. franklinii* as an animal of the tallgrass prairie (Van Petten and Schramm 1972, Krohne *et al.* 1973, Jones *et al.* 1983, Krohne and Schramm 1992, Benedict *et al.* 1996, Higgins *et al.* 2000, Pergams and Nyberg 2001). Because of this association, some have suggested a correlation between decreased availability of tallgrass prairie habitat—less than 4% of pre-European coverage is left (Samson and Knopf 1994)—and declining *S. franklinii* populations (Bowles 1981; Benedict *et al.* 1996; Pergams and Nyberg 2001, 2003). While it is true that there is considerable overlap between the geographic range of *S. franklinii* and the historic range of the tallgrass prairie environment (the forest-steppes and prairie ecoregion in Fig. 2), and while it is also true that the loss of tallgrass prairie habitat has undoubtedly negatively impacted *S. franklinii*, based on the review of the available literature I would contend that *S. franklinii* is not an animal that is strongly tied to tallgrass prairie habitat in the strictest sense. First, historically *S. franklinii* has occurred in nonprairie areas, particularly in the northern part of its range (Fig. 2). The northern exceptions aside, the fact that *S. franklinii* shares much of its distribution with the range of the former tallgrass prairie does not imply that tallgrass prairie is its focal habitat. Said another way, while *S. franklinii* could reasonably be described as an animal of the tallgrass prairie *region*, I feel that describing *S. franklinii* as an animal with a preference for tallgrass prairie *habitat* is much too restrictive. In describing *S. franklinii* habitat it is important to be cognizant of the effects of scale on perception. Although vegetation maps of the upper Midwest generally show two vegetation types, prairie and forest, a gradient exists between grasslands and woodlands where the habitats meld (Taft 1997). As Taft (1997) suggests, the portrayal of this sharp division is more a matter of convenience and is principally the result of the difficulty in mapping a habitat gradient. Unfortunately, this gradient that occurs at the interface of prairie and forest habitat—referred to as savanna, open woodland, or simply, savanna-like habitat (Taft 1997)—long has been ignored as an ecological community in North America.

To return to the issue of *S. franklinii* and tallgrass prairie habitat, Sargeant *et al.* (1993, p. 30) offered this view: "Little is known about the abundance of this species before settlement or about population trends after settlement. However, because of its specific habitat requirements, Franklin's ground squirrels probably were scarce or absent throughout the prairie before settlement, except in locations with brush, and probably were numerous in the aspen parkland." Indeed, Sargeant *et al.* (1993) found *S. franklinii* significantly more common at study sites within the aspen parkland zone than at those within the prairie zone. Although the comments of Sargeant *et al.* (1993) may suggest that *S. franklinii* historically was less common in the southern part of its geographic range where aspen parkland was absent, Taft (1997) clearly illustrates that other habitat was available for *S. franklinii* in the south in the form of oak-savannas. These oak-savannas were prevalent throughout Indiana, Illinois, Missouri, and much of Iowa and Wisconsin in presettlement times (Fig. 2.1 *in* Taft 1997). This understanding of the distribution of savanna-like habitat is reflected in Bailey's (1998) map of North American ecoregions, which includes the 'forest-steppe and prairie' ecoregion where tallgrass prairie is typically found (Fig. 2). Finally, while all evidence suggests that *S. franklinii* is most frequently associated with habitat that contains both grassy and woody components, it can occur in habitat that is dominated by grasses and forbs. However, based on my review of the data, I agree with Taft (1997) who included *S. franklinii* in a list of animals found in midwestern savanna-like habitats. Clearly, *S. franklinii* is described best as a species with an affinity for savanna-like habitats.

Agricultural associations. In addition to its use of natural, savanna-like habitats, many of the early accounts of *S. franklinii*, even accounts of prehistoric occurrence, indicate the squirrel's use of agricultural lands. From a distributional perspective, the clearing of forested areas for agriculture, which resulted in increased contact between grassland and woodland environments, allowed *S. franklinii* to expand its geographic range in some regions—particularly in the east (DeVos 1964). Agricultural modification of the land resulted in *S. franklinii* moving east into Ontario (Snyder 1938) and northeast in Minnesota (Hazard 1982; Robins 1970–1971), and allowed overall range expansions in both Iowa (Scott 1937) and Indiana (Lyon 1932).

Agriculture also affected the local abundance of *S. franklinii*. Because *S. franklinii* consumed newly planted corn and other grains, early agricultural practices provided an abundant source of food in close proximity to favorable habitat. Increased abundance of *S. franklinii* populations as a result of early agricultural practices were hinted at by Spurrell (1917, p. 283) who reported from Iowa, "This species was not as common in early days as it is now." The association of *S. franklinii* with agricultural lands also has had negative consequences for the species. As indicated in the accounts, when *S. franklinii* became noticeably numerous in agricultural areas, efforts were made either to eliminate them entirely, or at least to significantly reduce their numbers. This scenario even may have occurred at prehistoric agricultural settlements (Rhodes and Semken 1986).

Right-of-ways. Today, *S. franklinii* is frequently found along roadside or railroad right-of-ways, particularly in the southern portions of its geographic range (Haberman and Fleharty 1971; Gray 1972; Ellis 1982; Mumford and Whitaker 1982; Benjamin 1991; Johnson and Choromanski-Norris 1992; Lotter 1994; Hoffmann 1999; DeSanty-Combes 2001, 2002). Ellis (1982) concisely stated the reason for the high frequency of use of these right-of-ways by the squirrels in the southern portion of their geographic range: simply put, often right-of-ways represent the only available patches of habitat that meet the squirrel's needs. Gray (1972) echoed this sentiment for his area of Illinois when he stated that idle land was limited to streambanks, roadsides, railroads, and small woodlands along streams, the remainder of the land being utilized predominantly for intensive agriculture.

Modern agricultural practices in much of the midwestern U.S. maximize use of all available lands, thus fields are often plowed to fences or roads. Field-edges and fencerows that once provided valuable habitat for many different species of wildlife now, typically, are non-existent or quite "clean." In contrast, although typically roadside right-of-ways receive at least some level of mowing during summer months, in the absence of roadwork (such as lane widening) they are relatively undisturbed and often form ideal habitat for *S. franklinii*. This is particularly true of rural roads that often contain a mixture of grasses and forbs that grow unhindered throughout much of the summer, frequently complimented by shrub thickets and scattered trees. These factors, certainly apparent to Platt *et al.* (1973) in Kansas, led them to recommend that farmers leave native vegetation around field-edges and that the department of roads restrict mowing along roadside right-of-ways in order to increase *S. franklinii* habitat. Like roadside right-of-ways, railroad right-of-ways may serve as excellent habitat for *S. franklinii* in the lower Midwest. These areas, particularly when no longer in use and thus left undisturbed, result in a diverse mix of thick vegetation including grasses, shrubs, and trees in various stages of growth. Right-of-ways are almost certainly of less importance for the persistence of *S. franklinii* in the northern part of its geographic range where woodland edges and openings and aspen-parkland habitat remain relatively common.

Influences on Abundance

Although *S. franklinii* certainly appears to be capable of persisting at a site for many decades, especially large sites such as Delta Marsh in Manitoba (Sowls 1948, Tasmitt 1962, *pers. obs.* 2000, Hare 2004), more commonly the occurrence of the species at a specific location is highly variable. Several authors, reporting from Illinois (Kennicott 1857) and Wisconsin (Jackson 1961) in the south to Saskatchewan (Soper 1951, 1961b) in the north, have indicated that the squirrel may be present at a locality for some time—weeks, months, or even years—and then suddenly disappear. (See also Table 10 and the Appendix Table 1.) In the following paragraphs I convey how population

cycles, disturbance, and dispersal activities all may affect the squirrel's local abundance. Additionally, serving as the backdrop for these processes, I also suggest that *S. franklinii*'s primary use of savanna-like habitat has consequences for the persistence of its populations at local sites.

Population cycles and fluctuations. As indicated in the accounts, several authors have reported population fluctuations or cycles within *S. franklinii* (Sowls 1948, Haggerty 1968, Haberman and Fleharty 1971, Banfield 1974 Erlien and Tester 1984, Keith and Cary 1991). In some cases, cyclic lows reduce populations to the point where they disappear from the immediate area for a time (Erlien and Tester 1984), or are nearly brought to that point (Keith and Cary 1991). In those scenarios, the local site is repopulated, at least in part, by dispersers from nearby populations (Haggerty 1968, Erlien and Tester 1984). The factors responsible for these population fluctuations or cycles within *S. franklinii* remain unclear, but have been linked to snowshoe hare cycles with the squirrels serving as an alternate prey source for the hare's predators (Erlien and Tester 1984, Keith and Cary 1991). Although these reported population cycles within *S. franklinii* are limited to the northern part of the squirrel's geographic range (Minnesota, Manitoba, Alberta), where it overlaps with the distribution of the hare and thus lends some support to this hypothesis, irregular population peaks have been reported in Nebraska (Haberman and Fleharty 1971), outside the range of the hare. More long-term monitoring is needed to determine factors contributing to population fluctuations of *S. franklinii*.

Disturbance. The most obvious types of disturbance to populations of *S. franklinii* historically were attempts to exterminate them from a local area. Programs to eradicate squirrels were common around the turn of the nineteenth century (Bailey 1893) in the United States, and certainly resulted in dramatic fluctuations in local populations.

Disturbance of the squirrel's habitat also may cause their sudden departure from an area. Plowing of agricultural fields, which destroys burrows, will certainly cause any squirrels with burrows within the plowed field to leave—at least for a time. However, as Spurrell (1917) indicated, haying or mowing of tall grass also will cause squirrels to relocate to more favorable habitat. Loss of ground cover due to fire—prescribed or otherwise, is likely to cause *S. franklinii* to avoid the area until it is revegetated. I will discuss the impact of disturbance on the persistence of *S. franklinii* populations in greater detail in the "Conservation and Threats" section that follows.

Dispersal. Juvenile and male-biased dispersal is common in most ground squirrels (Holekamp 1984). Haggerty (1968), Ellis (1982), and Martin and Heske (2005) provided evidence that dispersal of *S. franklinii*, especially in juvenile animals, is probably quite common and accounts for both individual gains (through immigration to the site via dispersal) and losses (through emigration from the site via dispersal) in the local squirrel population. Population size and longevity in *S. franklinii* certainly is affected by dispersal activities, as it is in other animal populations (*in* Holekamp 1984). In the case of *S. franklinii*, because the squirrel lives in an increasingly fragmented environment—particularly in the southeastern portion of its geographic range, the survival of dispersing squirrels may be significantly lower than in historic times. Certainly, throughout much of the squirrel's geographic range, there are now greater distances separating areas of suitable habitat. Furthermore, the matrix between suitable areas of occupation is increasingly inhospitable to *S. franklinii*, as it has come to be dominated by agricultural monoculture, sterile suburban and urban landscapes, and everywhere a network of roadways. The failure of dispersers to encounter established populations may be a primary cause of the regional decline in *S. franklinii* in the southern portion of its geographic range. In effect, *S. franklinii* may exist as a dysfunctional metapopulation (Levins 1970) in this region where isolated populations (i.e., subpopulations) experience greater losses due to emigration than gains from immigration.

Effects of habitat. As already detailed, *S. franklinii* principally occupies savanna-like habitat. This habitat, by its very nature of being a composite of grasslands and woodlands, is habitat that is in flux (Skarpe 1992, Taft 1997); it moves from being dominated by one of these components to the other. In a simplistic sense, in the absence of disturbance (e.g., fire, wind-

storm, drought, or human habitat alteration) a savanna-like habitat will eventually come to be dominated by woodland habitat. Conversely, in the aftermath of disturbance, grassland habitat will dominate. In the case of *S. franklinii*, an occupied site—more specifically, a given habitat patch—may always be fluctuating in size as it responds to disturbance, or lack thereof. This obviously will have a bearing on the population dynamics within that habitat patch. If, for example, a given habitat patch becomes less favorable over time due to changes in vegetation, increased competition within the patch and increased rates of dispersal may result in a population decline at that site. This hypothesis—that the dynamic nature of savanna-like habitat occupied by *S. franklinii* directly influences its population dynamics—needs to be tested to see if it offers a plausible explanation for the variable nature of *S. franklinii* populations.

Conservation and Threats

It is apparent that *S. franklinii* has experienced declining populations in parts of its geographic range, particularly in the south (Platt *et al.* 1973; Bowles 1981; Johnson and Choromanski-Norris 1992; Lotter 1994; Anthony 1999; DeSanty-Combes 2002; Martin *et al.* 2003; Pergams and Nyberg 2001, 2003). The cause for these declines certainly includes human induced changes of local habitat, but may include other factors as well. In the following paragraphs, I will review known factors responsible for the decline of *S. franklinii* populations, speculate on additional factors, and discuss the current conservation concern for the species.

Habitat loss and disturbance. Although *S. franklinii* is not dependent on native or pristine habitat—the squirrel has occupied sites around landfills (Murie 1973) and in the midst of industrial settings (Lotter 1994)—loss of habitat nevertheless has contributed to its decline. As discussed earlier, in the southern portion of the squirrel's geographic range the availability of appropriate habitat is limited primarily to roadside and railroad right-of-ways. It is not surprising, then, to find that *S. franklinii* populations have declined in these regions of decreased habitat availability. Furthermore, while right-of-ways can provide suitable habitat for *S. franklinii*, they are often subject to disturbances that limit their usefulness. Frequent mowing and, more dramatically, lane-widening projects or track removal, may alter a site to the point that it is unsuitable for years to come Lotter (1994).

Not surprisingly, current *S. franklinii* habitat also is being lost through the construction of subdivisions, as documented by Lotter (1994). As urban sprawl continues to annex wildlife habitat, seemingly unabated, this trend will continue. To date the impacts of urbanization and sprawl have been greatest in the southeastern portion of the geographic range of *S. franklinii* where human populations are highest and where squirrel populations are of greatest conservation concern.

The connectedness of *S. franklinii* populations certainly contributes to the ability of the squirrel to recover from disturbances, whether human induced or otherwise. Erlien and Tester (1984) felt that when their study population of *S. franklinii* dropped to zero in 1965 and 1973, the site was likely repopulated from another population located within 1.5 km. Therefore, if distances that prohibit successful dispersal separate *S. franklinii* populations, then the prolonged existence of small populations—susceptible to various disturbances and other stochastic events—is undoubtedly tenuous. As already suggested, a metapopulation structure with declining subpopulations may aptly describe the existence of *S. franklinii* in portions of its geographic range.

Conservation status. In Indiana, where the distribution of *S. franklinii* has diminished to levels that warranted the listing of the species as "Endangered," the ecological importance of this decline may not be as significant as elsewhere in the species' geographic range. Although Lotter (1994) reported a continued reduction in *S. franklinii* populations since Johnson and Choromanski-Norris (1992), she still found the squirrel at eight sites in three counties, whereas Bailey (1893) reported *S. franklinii* from only two sites in extreme western Indiana. In short, it is likely that *S. franklinii* expanded its range in Indiana as a result of early agricultural practices and subsequently has declined as a result of habitat loss. The continued decline of the species in Indiana almost certainly is reflective of a general trend of increasing urbanization with concomitant habitat loss—especially in the heavily populated northwest corner of the state. These changes of the Indiana landscape should be of ecological concern, because they will affect many of the state's native organisms. However, in regard to *S. franklinii* in Indiana, the species might best be considered rare in the state—as are many other species at the periphery of their geographic ranges.

Elsewhere in the southern portion of its geographic range, particularly in Illinois, Iowa, Kansas, and Missouri, *S. franklinii* populations may be occurring well below historic levels. Unfortunately, difficulties in detecting the presence of *S. franklinii*, coupled with its patchy distribution and irregular patterns of occurrence, make surveying for the species challenging and assessing declines even more problematic. With the exceptions of Illinois and Missouri, both of which have been surveyed intensely and systematically for *S. franklinii* in recent years (Hoffmann 1999; DeSanty-Combes 2001, 2002; Martin *et al.* 2003), declines in *S. franklinii* populations elsewhere in the south remain circumstantial, but quite likely. In my own limited efforts, I failed to locate any extant populations of *S. franklinii* in Iowa or Kansas, nor was I able to ascertain the existence of active populations residing within these states from regional biologists.

As I detailed in earlier sections, the availability of appropriate habitat certainly is most limited in the southern portion of the squirrel's geographic range where land use is most intense. In these areas where *S. franklinii* is limited in occurrence primarily to roadside and railroad right-of-ways, the species is extremely susceptible to additional disturbances. The conservation concern that has developed for *S. franklinii* in Illinois is certainly warranted, as it should be in Iowa, Kansas, and Missouri, at least until further data suggest otherwise.

Elsewhere, particularly in parts of Minnesota, North Dakota, Manitoba, and Saskatchewan, the region where *S. franklinii* historically has been common, the same remains true today. In appropriate locations, *S. franklinii* currently ranges from common to abundant in this region, a fact I verified through personal experience in May and June 2000. The greater prevalence of savanna-like habitat in the northern part of the squirrel's range undoubtedly contributes to its commonness in this region, as alluded to earlier by Sargeant *et al.* (1993). Loss of *S. franklinii* habitat as a result of human activity is also certainly less in the northern portion of the squirrel's geographic range, which is populated at lower human densities.

CONCLUSIONS

S. franklinii is a species that most frequently is associated with habitat characterized by a mixture of grassy and woody vegetation, that is, savanna-like or parkland habitat. The species has had an affinity for this type of habitat throughout its geographic range in recent, historic, and even prehistoric times. As a result of its association with agricultural lands, *S. franklinii* has expanded its geographic range in some areas but also has been subject to eradication programs that have resulted in its local extirpation. Populations of *S. franklinii* are subject to marked fluctuations, the reasons for these being not entirely clear, but which probably are influenced by local disturbances in addition to regular dispersal events. In the southern part of its geographic range, *S. franklinii* is limited in its occurrence principally to roadside and railroad right-of-ways as a result of a lack of other suitable habitat. In these southern regions, *S. franklinii* is justifiably of conservation concern. I suggest that more detailed surveys for the species (such as those that have recently occurred in Illinois and Missouri) take place in Iowa and Kansas.

ACKNOWLEDGMENTS

I am greatly thankful for the assistance of the many curators and collections managers that offered me aid during my on-site visits to museums, and that processed loans of museum specimens. Every museum I utilized is individually named in the Appendix. I also thank the archive staff at the Smithsonian's National Museum of Natural History for their assistance during my visit. I am grateful for the guidance provided by my doctoral committee, including Dr. Gwen Bachman, Dr. Patricia Freeman, Dr. Guillermo Ortí, Dr. Edward J. Peters, and particularly Dr. Hugh Genoways, who served as my academic advisor throughout my doctoral program. Special thanks to two anonymous reviewers and to Dr. Edward J. Heske and Dr. Oliver R. W. Pergams for their comments and suggestions on this manuscript. My wife, Dr. Erin Huebschman, deserves special thanks for her assistance with many aspects of this project. Financial support for this research was provided in part by the following sources: Center for Great Plains Studies, American Museum of Natural History, Theodore Roosevelt Memorial Funds, University of Nebraska-Lincoln Initiative in Ecology and Evolutionary Biology, and the Warren F. and Edith R. Day Dissertation Travel Funds.

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APPENDIX

Given below is the list of 732 Franklin's ground squirrels, *Spermophilus franklinii*, examined and geographically plotted in Figure 2. Specimens are arranged by country of origin, province or state, and county—when given, all in alphabetical order. A key to museum codes (Hafner et al. 1997) follows the list of specimens.

CANADA

Alberta: Athabasca area, T66 R24 Sec. 25, 1 (UMMZ); 1 mi N, 9 mi W Athabasca, 1 (PMA); Beaverhill Lake, 3 (PMA); Belvedere, 1 (CMN); 1 1/2 mi SSW Blackfalds, 1 (MSU); Camrose, 2 (ROM); Camrose, Pelican Lake, 1 (ROM); Chain Lakes, 2 (PMA); Chain Lakes Recreation Area campground, T69N, R23W, Sec. 7, NW 1/4, 1 (UNSM); Beaver River, near Cold Lake, 1 (CMN); Driedmeat Lake, 3 (ROM); Edmonton, 3 (CMN); 2 (ROM); Lac la Nonne, 4 (CMN); Battle River S of Galahad, 1 (CMN); Marwayne, 1 (CMN); near Mayerthorpe, 1 (PMA); Meanook, 1 (PMA); Meeting Creek, 1 (CMN); Morinville, 2 (PMA); Raft Lake, 1 (PMA); Red Deer, 1 (CMN); N Red Deer, Red Deer River, 1 (CMN); Red Lodge, 1 (ROM); Rochon Sands Provincial Park, 1 (PMA); 1 (UNSM); Sandy Lake, 1 (CMN); Sturgeon River, 25 mi N of Edmonton, 2 (NMNH).

Manitoba: Aweme, 2 (MMMN), 4 (ROM); Birtle, 1 (MMMN); Carberry, 1 (CMN), 3 (NMNH); 1 km N Cromer, 1 (MMMN); Dauphin, 1 (CMN); Delta, 1 (CMN), 1 (MMN), 2 (MMNH), 11 (MUMZ), 2 (NMNH), 2 (UMMZ), 1 (UWZM); Delta Marsh, 3 (MMMN); Delta Marsh, University Field Station, 8 (MMMN), 1 (UNSM); 1.5 mi W Delta, 1 (ROM); 3 mi E Delta, 1 (ROM); S of Duck Mountain Forest Reserve, 1 (CMN); 3.2 km N, 9.6 km W Dugald, 1 (MMMN); 5.8 km S, 1.6 km E Hadashville, 2 (MMMN); 13.5 km N, 29.6 km W Hodgson, vicinity of Matootoo Lake, 1 (MMMN); Huns Valley, 1 (ROM); 10 km N Libau, 2 (MMMN); Manitoba House, 1 (NMNH); 6.4 km N, 0.8 km W Margaret, 2 (MMMN); Neepawa, 2 (ROM); 13 km S, 7 km W Oak Lake, 2 (MMMN); 11.2 km S Oak Lake, 1 (MMMN); Patricia Beach, 1 (MMMN); Pinawa, Whiteshell Nuclear Research Est., 30 (MMMN); Portage la Prairie vicinity, 1 (ROM); Red Rock Lake, near Rennie, 2 (CMN); Rennie, 1 (MUMZ); Riding Mountain National Park, 1 mi S of S gate, 2 (YPM); Riding Mountain National Park, Lake Andy campground, 1 (YPM); 3.2 km N, 3.2 km E Roseisle, 2 (MMMN); Shoal Lake, 1 (CMN); 11 km N, 4 km E Sprague, 4 (MMMN); 3.2 km NW St. Ambroise, 1 (MMMN); 4.8 km N, 4.8 km W St. Ambroise, 1 (MMMN); St. Ambroise Beach, 3 (MMMN); St. Charles, 1 (ROM); Swan River, 1 (CMN); The Pas, 2 (CMN), 1 (YPM), 1 (MMMN); 4 km SW The Pas, 1 (CMN); University Field Station, 1 (MMMN); Winnipeg, 3/4 mi E on Paul Blvd, 1 (MMMN); Winnipeg, Brockville St. and Wilker Ave., 1 (CMN); Winnipeg, vicinity of Springfield sanitation land fill, 1 (MMMN); Winnipeg, Deer Lodge, 1 (ROM); Winnipeg, St. Vitae, 1 (ROM); Winnipeg, 3 (MMMN), 1 (NMNH), 2 (ROM).

Ontario: 1 km NE of Crozier, Crozier TSP, Fort Frances Dist., 1 (ROM); 3 km NW of Stratton, Morley TSP, Fort Frances Dist., 3 (ROM); Long Sault Rapids, Study Site 1, Roseberry TSP, Fort Frances Dist., 1 (ROM); Keewatin, Kenora Dist., 1 (ROM); Royal Lake, 25 mi W of Kenora, Kenora Dist., 1 (ROM); Rainy River, 8 (ROM); Rainy River Dist., 1 (ROM); Carpenter Twp, Rainy River Dist., 1 (ROM); N of Rainy R., Curran TSP, Rainy River Dist., 1 (ROM); 1 1/2 mi upstream from Lake of the Woods on Rainy River, 1 (ROM).

Saskatchewan: Broadview, 2 (CMN); Carlton House, 4 (NMNH); 6 mi S Dorintosh, 2 (CMN); Douglas Provincial Park, Middaugh campground, 1 (UNSM); Dundurn, 2 (ROM); Emma Lake, 2 (CM); Emma Lake, Prince Albert Dist., 2 (ROM); 3 (UMMZ); Fort Carlton, 4 (ROM); Good

Spirit Lake Provincial Park, Aspen campground, 2 (UNSM); Indian Head, 5 (CMN); 8 (ROM); Indian Head, Assiniboia, 3 (NMNH); 1 mi W of Lebret, Qu'Appelle Vy., 1 (UMMZ); South arm, Last Mountain Lake, 1 (CMN); Moose Mountain Provincial Park, T10N, R3W, Sec. 24, SE 1/4, 1 (UNSM); Oxbow, 1 (NMNH); Prince Albert, 1 (FMNH); 7 mi S, 2 mi W Prince Albert, 46N, 27W, Sec. 36, NE 1/4, 1 (UNSM); Rokeby, 1 (ROM); Watson, 2 (ROM); Wingard, 5 (NMNH); Katepwe Lake, 2 (ROM); TWP 31, RGE 28, Sec. 6, SW 1/4, 1 (UNSM).

UNITED STATES

Illinois: Carroll Co.: Mount Carroll, 1 (NMNH); Champaign Co.: 2 1/2 mi SE Broadlands, 1 (CM); Champaign, 1 (ISUVC); 1 mi S Champaign, 1 (UIMNH); 1 mi W Champaign on Route 150, 1 (UIMNH); 3 mi S Champaign, 3 (UIMNH); 10 mi N and 2 mi W Champaign, 1 (UIMNH); Mayview, 2 (UIMNH); 4/10 mi W Mayview, 2 (UIMNH); 1.2 mi E Mayview, 1 (UIMNH); 1 1/2 mi E Mayview, 1 (UIMNH); 2 mi E of Mayview, 3 (UIMNH); Mayview Cemetery, 1 (UIMNH); Vic. Parkland College, 1 (UIMNH); 1.2 mi W Saint Joseph, 4 (UIMNH); 1 1/2 mi W Saint Joseph, 1 (UIMNH); Saint Mary's Cemetery, 1 1/2 mi S Champaign, 1 (UIMNH); 2 mi S Savoy, 1 (UIMNH); Seymour, 1 (UIMNH); Urbana, 4 (INHS); E of Urbana, 1 (INHS); Urbana township, 1 (UIMNH); Willard Airport, 1 (UIMNH); Christian Co.: 1/2 mi E Stonington, 1 (UIMNH); Coles Co.: Vic. Mattoon, 1 (UIMNH); Cook Co.: Chicago, 1 (CHAS), 1 (YPM); Chicago Heights, 1 (FMNH); Lemont, 1 (CHAS); West Northfield, 2 (NMNH), 1 (UMMZ); Western Springs, 49th and Fair Elms Ave., 1 (MSB); DuPage Co.: Glen Ellyn, 1 (CHAS); Milton Twp, 3 (CHAS); Fulton Co.: 3 mi W Canton, 1 (UIMNH); 4 mi NW Canton, 1 (UIMNH); 1 mi NW Norris, 2 (UIMNH); Hancock Co.: Warsaw, 1 (FMNH), 3 (NMNH); Kane Co.: 3 mi W Geneva, 1 (FMNH); Lake Co.: Fox Lake, 1 (FMNH); Grays Lake, 7 (CHAS); 1.6 mi N of Mundelein on city limits on Hwy 45, 1 (FMNH); LaSalle Co.: Earlville, 1 (INHS); Livingston Co.: 1 mi S Strawn, 1 (UIMNH); McLean Co.: 1 mi S of Route 9, 1 mi W of Bloomington city limits, 1 (ISU); 4 mi SW of Bloomington city limits on Gulf Mobile and Ohio R. R., 1 (ISU); 6 mi NE Normal, 1 (ISU); 7.5 mi NE Normal, 3 (ISU); Ogle Co.: Oregon, 1 (INHS); Piatt Co.: 1 mi N Monticello (highway), 1 (UIMNH); Vermillion Co.: 10 mi W Danville, 1 (UIMNH); Will Co.: Joliet, 1 (UMMZ); near Lemont (in Cook County), 1 (CHAS).

Indiana: Benton Co.: 1 mi S of Atkinson, 1 (NMNH); Fulton Co.: 3 mi W, 1 mi N Rochester, 1 (NMNH); Jasper Co.: 6 mi N, 10 mi E Rensselaer, 1 (NMNH); Lake Co.: Miller, 2 (FMNH); LaPorte Co.: At interchange of Indiana toll road and U. S. 421, 1 (NMNH); Marshall Co.: Tyner, 1 (NMNH); Newton Co.: Lake Village, 6 (UMMZ); Morocco, 2 (ISUVC); Mount Ayr, 3 (NMNH); Porter Co.: Dune Acres, 1 (CHAS); Dunes State Park, 1 (JMM); St. Joseph Co.: 3 mi S of North Liberty, 1 (ISUVC); 2 1/2 mi W, 1 mi S of North Liberty, 1 (NMNH); Walkerton, 1 (NMNH); Tippecanoe Co.: Klondike, 1 (JMM); 1 1/2 mi S of Romney, 1 (NMNH); Wabbash Township, 1 (NMNH); White Co.: Shafer Lake, 2 (UMMZ).

Iowa: Butler Co.: T90N, R18W, Washington Township, 1 (HMNH); Clay Co.: 9 (UMMZ); Webb, 3 (AMNH); Crawford Co.: Dow City, 1 (CHAS); Des Moines Co.: Burlington, 1 (NMNH); Dickinson Co.: Milford, 1 (UMMZ); Grundy Co.: 5 mi W Grundy Center, 1 (IOWA); Jasper Co.: 1 mi N Prairie City, 1 (KU); Johnson Co.: Iowa City, 1 (AMNH); Louisa Co.: 1 (IOWA); Mahaska Co.: 1 1/2 mi S, 2 mi E New Sharon, 2 (KU); 5 mi N Oskaloosa, 1 (KU); Marion Co.: 1 1/2 mi S, 1 1/2 mi W Pella, 1 (IOWA); Mills Co.: 1 mi N, 5 mi W Malvern, 1 (BVC); Monona Co.: 2 mi N Pisgah, 1 (BVC); 1 mi N, 3 1/2 mi W Whiting, South Badger Lake, 1 (IOWA); Montgomery Co.: 11.1 mi E Red Oak, 1 (MSB); Muscatine Co.: Conesville, 1 (NMNH); Story Co.: Ames, 3 (NMNH); Franklin Township, 1 (MSU).

Kansas: Allen Co.: 5 1/2 mi N of Moran, 1 (KU); Douglas Co.: 2 1/2 mi NW Eudora, 1 (KU); Lawrence, 3 (KU); KU campus, Lawrence, 1 (KU); 1 1/2 mi E, 1 3/4 mi N Lawrence, 1 (KU); 2 mi S Lawrence, E. Haskel Bottoms, 1 (CMN); 2 mi N, 1.6 mi E Douglas Co. courthouse, Lawrence, 1 (KU); 2 mi E, 2 mi N Lawrence, 1 (KU); near Lawrence, 2 1/2 mi S, 1/4 mi W No. 6 school house, S side of Wakarusa Creek, 1 (KU); 3 mi SW Lawrence, 1 (KU); 3 mi S Lawrence, 1 (KU); 3 mi N Lawrence, 1 (KU); 3 1/2 mi S Lawrence, 1 (KU); 4 mi N of Lawrence, between Teepee junction and R. R. tracks, 2 (KU); 7 1/2 mi SW Lawrence, 1 (KU); Greenwood Co.: Hamilton, 1 (KU); Jewell Co.: 20 mi E Smith Center, 1 (KU); T15, R7W, Sec. 14, NW 1/4, 3 (MHP); McPherson Co.: Smokey Hill River, 1 mi S, 1/2 mi W Lindsborg, 2 (KU); 1/2 mi E McPherson, 4 (KU); Mitchell Co.: 3 1/2 mi W, 1/2 mi S Beloit, 1 (KU); Phillips Co.: 1 1/2 mi W Glade, T4S, R18W, Sec. 22, SW 1/4, 1 (MHP); 1 mi N, 6 1/4 mi W Kirwin, T4S, R17W, Sec. 21, S 1/2, 1 (MHP); 1 3/4 mi S, 4 mi W Kirwin, T5S, R17W, Sec. 1, SW 1/4, 1 (MHP); 10.8 mi N Phillipsburg, 1 (MHP); Pottawatomie Co.: 3 mi NW of St. Mary's, 1 (KU); Onaga, 1 (NMNH); Republic Co.: Agenda, 1 (KU); Riley Co.: Manhattan, 1 (KU); Woodson Co.: Neosho Falls, 3 (KU).

Minnesota: Beltrami Co.: 1/4 mi NE Redby, 4 (MMNH); Big Stone Co.: Big Stone Lake State Park, T122N, R47W, Sec. 10, SE 1/4 of SE 1/4, 1 (MMNH); Ortonville, 11 (NMNH); Ortonville, Elk River, 1 (CMN); Blue Earth Co.: 3 mi S Minnesota Lake, 1 (SHMC); Rapidan, 1 (INHS); Cass Co.: Cass Lake, 2 (NMNH); 2 mi SE Winnie Dam, T145N, R27W, Sec. 35, E 1/2, Chippewa Forest, 1 (MMNH); Clay Co.: 1 1/2 mi W Buffalo River State Park, 1 (UIMNH); Moorhead (Bosshard Farm), 1 (CM); T141N, R46W, Sec. 24, NW 1/4, 1 (MMNH); Clearwater Co.: W of Itasca Park, 1 (MMNH); Biological Station, Itasca Park, garbage pile, 1 (MMNH); Itasca State Park, 1 (JMM); Grant Co.: 3 mi NW of Barrett, 1 (UMMZ); 4 mi NW of Barrett, 1 (UMMZ); Setan WPA, T130N, R43W, Sec. 25, NE 1/4, 1 (UNSM); Stony Brook Township, T130N, R43W, Sec. 24, 1 (UNSM); Hennepin Co.: Ft. Snelling, 1 (FMNH), 4 (NMNH); Hubbard Co.: Lake Alice Store, T143N, R35W, Sec. 22, NE 1/4 of SW 1/4, 5 (MMNH); Isanti Co.: 5 mi E of Hwy 65 along Cty Rd. 12, T34N, R22W, Sec. 18, 1 (MMNH); Kandiyohi Co., T121N, R35W, Sec. 27, NW 1/4, 1 (MMNH); Lac Qui Parle Co.: 1 mi N, 9 mi E Bellingham, T119N, R43W, Sec. 6, NW 1/4 of NW 1/4, 1 (MMNH); Madison, 2 (MCZ); Lake of the Woods Co.: Williams, 1 (KU), 2 (MMNH); LeSuer Co.: T112N, R24W, Sec. 23, 1 (MMNH); Mahnomen Co.: 8 mi E Mahnomen, 1 (UMMZ); Marshall Co.: Holt, 1 (MMNH); Morrison Co.: Cushing, 2 (MSB); Ottertail Co.: Fergus Falls, east of town, 2 (MMNH); Lake Lizzie, 1 (CM); Pine Co.: Bruno, 1 (MMNH); Polk Co.: 3 mi S, 7 mi E of Crookston, T149N, R45W, Sec. 17, Pankratz Prairie, 2 (MMNH); Pope Co.: 7 mi S of Glenwood, 1 (MMNH); Rice Co.: Northfield, 1 (MMNH); Shieldsville Twp., Sec. 12, 1 (MMNH); Roseau Co.: Warroad, 1 (MMNH); Sherburne Co.: Elk River, 11 (NMNH), 2 (ROM), 1 (UMMZ), 1 (UWZM); Sibley Co.; 1 mi N of Gibbon, 1 (MMNH); St. Louis Co.: 1/4 mi E Adolph, 1 (MHP); 8 mi S, 1 mi W Hoyt Lakes, T57N, R14W, Sec. 19, SE 1/4, 1 (MMNH); Saginaw, 3 (KU); Traverse Co., Brown's Valley, 3 (MMNH); near Brown's Valley, 5 (NMNH); 6 mi W of Wheaton, 1 (MMNH); Wadena Co.: T134N, R35W, Sec. 8, NE 1/4, 1 (MMNH); Wilkin Co.: 3 mi S of Rothsay, 1 (MMNH); Wright Co.: Maple Lake, 1 (MMNH).

Missouri: Adair Co.: 1 mi N LaPlata, 1 (NEMSU); 2 mi SE Millard, 1 (CM), 2 (NEMSU); Buchanan Co.: St. Joseph, 1 (MUMZ); 1 mi E St. Joseph, 2 (MUMZ); Caldwell Co.: Hamilton, 1 (MUMZ); Chariton Co.: Swan Lake National Wildlife Refuge, along railroad dump, 2 (MUMZ); Clark Co.: 3 mi W, 2 mi S Alexandria, 2 (NEMSU); 1 mi E Medill, 1 (NEMSU); Clinton Co.: Trimble Wildlife Area, 2 (MUMZ); Knox Co.: 3 mi SE Knox City (Hwy 6), 1 (NEMSU); Lafayette Co.: Wellington, 1 (MUMZ); Macon Co.: 4 mi N Macon, 2 (CM); 4 mi N Macon, 1 (NEMSU); 8 mi N Macon, 1 (CM).

Nebraska: Antelope Co.: Neligh, 1 (UNSM); 1/4 mi N, 1/2 mi W Oakdale, 1 (UMMZ); Boone Co.: Albion, west road of fairgrounds, 1 (MHP); near Albion, 1 (MHP); 1/2 mi W, 1/2 mi S of Albion, 1 (MHP); 6 mi E of Albion, 1 (MHP); Buffalo Co.: Kearney, 1 (NMNH); Custer Co.: 1 mi S Gavin, 1 (UMMZ); Dawson Co.: E of Gothenburg, 1 (UNSM); Dodge Co.: Ames, 1 (NMNH); Douglas Co.: Omaha, 1 (YPM); Omaha, 108th and E St. intersection, 2 (MSB); Omaha, Henry Doorly Zoo, 3 (UNSM); Stolley Prairie, T15N, R11E, Sec. 15, NW 1/4, 3 (UNSM); Garfield Co.: 3 mi N, 4 1/2 mi W Burwell, 1 (VMKSC); Harlan Co.: 1 mi S, 0.5 mi E of Orleans, 1 (VMKSC); Hitchcock Co.: 6 mi E of Palisade, 1 (VMKSC); Hooker Co.: Kelso, 8 (UMMZ); Knox Co.: Niobrara, 1 (NMNH); Verdigre, 1 (NMNH); Lancaster Co.: Lincoln, 1 (MVZ); Lincoln, Capital Beach Lake, 1 (NMNH); Lincoln, Mopak bike trail, T10N, R7E, Sec. 26, NW 1/4, 2 (UNSM); Lincoln Co.: North Platte, 1 (MSB); Nemaha Co.: 1/2 mi N, 1 mi E Peru, 1 (MHP); Platte Co.: Columbus, 2 (NMNH); Red Willow Co.: 2.4 mi W Cambridge, 1 (VMKSC); Richardson Co.: Falls City, 1 (KU); 3 mi S Rulo, 1 (KU); Sarpy Co.: Chalco Hills Recreation Area, T14N, R11E, Sec. 23, SW 1/4, 1 (UNSM); Thurston Co.: 1 mi S Winnebago, 1 (KU); Webster Co.: Red Cloud, 1 (UNSM).

North Dakota: Barnes Co.: Kathryn, 1 (NMNH); Benson Co.: Minnewaukan, 1 (FMNH), 1 (UWZM); Burke Co.: Lostwood National Wildlife Refuge headquarters, T160N, R91W, Sec. 35, NW 1/4, 3 (UNSM); Cass Co.: Fargo, 1 (NMNH); Harwood, 2 (NMNH); Dickey Co.: Oakes, 3 (FMNH), 3 (NMNH); Foster Co.: Bordulac, 2 (UWZM); Grand Forks Co.: 3 mi E of Emerado, 2 (MMNH); Grand Forks, 1 (NMNH); 4 (ROM); Larimore, 2 (NMNH); Kidder Co.: 1/2 mi N Pettibone, 1 (UMMZ); LaMoure Co.: LaMoure, 1 (NMNH); Nelson Co.: Stump Lake, 2 (NMNH); Pembina Co.: Pembina, 12 (NMNH), 1 (YPM); Walhalla, 2 (NMNH); Ramsey Co.: Devil's Lake, 3 (UMMZ); Richland Co.: 5 mi NE Fairmount, near Sioux River, 13 (NMNH); Rolette Co.: 1 mi N Dunseith, 1 (MVZ); 5 mi E Dunseith, 1 (MVZ); 7 mi NE Dunseith, 2 (MVZ); Turtle Mountains, Lake Upsilon, 2 (UMMZ); Sargent Co.: Tewaukon National Wildlife Refuge, 12 (UNSM); Stutsman Co.: Arrowwood National Wildlife Refuge, T143N, R63W, Sec. 6, NW 1/4, 1 (UNSM); 3 mi NW Buchanan, 1 (UCM); James River, 10 mi S Jamestown, 5 (UCM); Walsh Co.: Grafton, 2 (UNSM); Ward Co.: Baden, 1 (MSB), 1 (KU).

South Dakota: Bon Homme Co.: Scotland, 1 (NMNH); Brown Co.: 2 mi N, 3 mi W of Houghton, 2 (KU); Clay Co.: 6 1/2 mi N, 1 1/2 mi W Vermillion, 1 (MSB); Day Co.: 1 (MSU); Waubay National Wildlife Refuge, 3 (UIMNH); Webster, 3 (CHAS); Marshall Co.: Fort Sisseton, 5 (NMNH); Roy Lake State Park, 5 (KU); Moody Co.: Flandreau, 1 (NMNH); Roberts Co.: 4 mi S of Blackmer (in North Dakota), 4 (NMNH); Trip Co.: Dog Ear Lake, 1 (UMMZ); 5 mi SE Colome, 1 (UMMZ); Union Co.: 4 1/2 mi NW Jefferson, 1 (MSB).

Wisconsin: Columbia Co.: Portage, 1 (UWZM); Dane Co.: Madison, University of Wisconsin Arboretum, 2 (UWZM); Dodge Co., Beaver Dam, 6 (UWZM); Portage Co., 2 mi S Junction City, 1 (UWSP); T23N, R7E, Sec. 2, N 1/2 of SE 1/4, 1 (UWSP); 1 mi W Hwy N, 1 (UWSP); Racine Co., Racine, 1 (NMNH); Rock Co., Milton, 1 (UWZM); Walworth Co., Delavan, 2 (CHAS); 4 (NMNH); Lane's Mill, 5 (AMNH); Waukesha Co., T6N, R19E, Sec. 14, NW 1/4 of SW 1/4, 1 (MMNH); Wood Co., 3/4 mi SE Arpin, 1 (UWSP).

Museum Key: American Museum of Natural History (AMNH); Buena Vista College (BVC); Canadian Museum of Nature (CMN); Carnegie Museum of Natural History (CM); Chicago Academy of Sciences (CHAS); Earlham College, Joseph Moore Museum (JMM); Fort Hays State University, Sternberg Museum of Natural History (MHP); Harvard University, Museum of Comparative Zoology (MCZ); Illinois Natural History Survey (INHS); Illinois State University (ISU); Indiana

State University (ISUVC); Kearney State University, Vertebrate Museum (VMKSC); Luther College, Sherman A. Hoslett Museum of Natural History (HMNH); Manitoba Museum of Man and Nature (MMMN); Michigan State University Museum (MSU); Provincial Museum of Alberta (PMA); Royal Ontario Museum (ROM); The Field Museum (FMNH); Truman State University (NEMSU); United States National Museum of Natural History (USNM); University of California, Berkeley, Museum of Vertebrate Zoology (MVZ); University of Colorado Museum (UCM); University of Illinois, Museum of Natural History (UIMNH); University of Iowa, Museum of Natural History (IOWA); University of Kansas, Museum of Natural History (KU); University of Michigan, Museum of Zoology (UMMZ); University of Minnesota, James Ford Bell Museum of Natural History (MMNH); University of Missouri, Museum of Zoology (MUMZ); University of Nebraska State Museum (UNSM); University of New Mexico, Museum of Southwestern Biology (MSB); University of Wisconsin, Stevens Point, Museum of Natural History (UWSP); University of Wisconsin, Zoological Museum (UWZM); Yale University, Peabody Museum of Natural History (YPM).

APPENDIX TABLE 1. Tabulation of specific accounts of Franklin's ground squirrel, *Spermophilus franklinii*, reported in the text that address *S. franklinii* populations and habitat use. Citations are arranged by the section in which they occur. Citations are taken from both text and tables appropriate to that section.

		Characterization of population(s)			Characterization of habitat		
Year	Section in which citations occur	Common, abundant, increasing, or a pest	Uncommon, rare, or declining	Fluctuating or variable in occurrence	Prairie[1]	Savanna[2]	Woodland[3]
Pre-1950	North America	Coues and Allen 1877				Coues and Allen 1877	
	Canada					Soper in Sowls 1948	
	Alberta	Preble 1908	Loring *in lit.*, NMNH archives, 1894			Preble 1908	
			Soper 1921			Soper 1921	
	Manitoba	Seton 1910 Bird 1927 Criddle 1929 Green 1932 Soper 1946		McLeod 1933 Sowls 1948		Seton 1910 Sowls 1948	Bird 1927
	Ontario				Snyder 1938		
	Saskatchewan	Loring *in lit.*, NMNH archives, 1895				Richardson 1829 Loring *in lit.*, NMNH archives, 1895	
	United States					Bailey 1893	

Continued on next page

Appendix Table 1 continued

Year	Section in which citations occur	Characterization of population(s)			Characterization of habitat		
		Common, abundant, increasing, or a pest	Uncommon, rare, or declining	Fluctuating or variable in occurrence	Prairie[1]	Savanna[2]	Woodland[3]
Pre-1950	Illinois	Kennicott 1855	Coleman *in lit.*, NMNH archives, 1892	Kennicott 1857	Kennicott 1855 Wood 1910	Kennicott 1857	
	Indiana		Lyon 1932 Lyon 1936		Hahn 1909 Lyon 1932 Lyon 1936		
	Iowa	Allen 1871 Van Hyning and Pellet 1910 Ruthven and Wood 1912 Gabrielson 1921	Coleman *in lit.*, NMNH archives, 1892	Stoner 1918	Spurrell 1917	Stoner 1918	
	Kansas	Bailey 1893 Kellogg 1915 Black 1937	Knox 1875 Lantz 1905		Lindsdale 1928	Kellogg 1915 Black 1937	
	Minnesota	Bailey 1888	Herrick 1892	Swanson *et al.* 1945	Bailey 1888	Bailey 1888	Augstin *in lit.*, NMNH archives, 1930

	Herrick 1892	Bailey 1893		Herrick 1892	
	Johnson 1930	Murie *in lit.*, NMNH archives, 1919 Bailey *in lit.*, NMNH archives, 1932		Johnson 1922 Johnson 1930 Bailey *in lit.*, NMNH archives, 1932 Swanson *et al.* 1945	
Nebraska	Aughey 1880 Coleman *in lit.*, NMNH archives, 1892 Bailey *in lit.*, NMNH archives, 1893 Cary *in lit.*, NMNH archives, 1903 Swenk 1908	Warren 1875 Bailey *in lit.*, NMNH archives, 1894 Lautz *in lit.*, NMNH archives, 1910	Bailey 1893	Aughey 1880 Coleman *in lit.*, NMNH archives, 1892	
North Dakota	Coues and Allen 1877 Bailey 1888 Williams *in lit.*, NMNH archives, 1912	Murie *in lit.*, NMNH archives, 1919	Fisher *in lit.*, NMNH archives, 1893	Williams *in lit.*, NMNH archives, 1912 Sheldon *in lit.*, NMNH archives, 1915	Bailey 1888 Bailey 1893 Fisher *in lit.*, NMNH 1893

Continued on next page

Appendix Table 1 continued

Year	Section in which citations occur	Characterization of population(s)			Characterization of habitat		
		Common, abundant, increasing, or a pest	Uncommon, rare, or declining	Fluctuating or variable in occurrence	Prairie[1]	Savanna[2]	Woodland[3]
		Eastgate *in lit.*, NMNH archives, 1912				Williams *in lit.*, NMNH archives, 1912	
		Bailey *et al.* 1914				Eastgate *in lit.*, NMNH archives, 1912	
		Sheldon *in lit.*,				Bailey *et al.* 1914	
		NMNH archives, 1915					
		Kellogg *in lit.*, NMNH archives, 1915				Kellogg *in lit.*, NMNH archives, 1915	
	South Dakota	Bailey *in lit.*, NMNH archives, 1893					
		Over and Churchill 1945					
	Wisconsin		Bailey 1893	Snyder 1902	Strong 1883	Hollister 1908	
				Jackson 1908	Snyder 1902	Schmidt 1931	
				Hollister 1908	Jackson 1908		
Post-1950	North America		Pergams and Nyberg 2003		Hall and Kelson 1959	Murie 1999	
					Pergams and Nyberg 2003		
					NatureServe 2004		

Canada	Banfield 1974		Banfield 1974		Banfield 1974
Alberta		Smith 1993	Soper 1964		Soper 1964
			Keith andCary 1991		Murie 1973
					Keith and Cary 1991
					Smith 1993
Manitoba	Soper 1961a	Soper 1953			Tamsitt 1962
	Tamsitt 1962	Wrigley 1974			Iverson and Turner 1972
					Wrigley 1974
					Burachynsky and Galloway 1985
					Reichardt and Galloway 1994
Saskatchewan			Soper 1951		Soper 1951
			Soper 1961b		Beck 1958
Illinois	Hoffmeister and Mohr 1957	Scott *et al.* 1959		Anderson 1951	Hoffmeister and Mohr 1957
	Scott *et al.* 1959	Van Petten and Schramm 1972		Gray 1972	Martin and Heske 2004
		Panzer and Schipp 1986		Van Petten and Schramm 1972	

Continued on next page

Appendix Table 1 continued

Year	Section in which citations occur	Characterization of population(s): Common, abundant, increasing, or a pest	Characterization of population(s): Uncommon, rare, or declining	Characterization of population(s): Fluctuating or variable in occurrence	Characterization of habitat: Prairie[1]	Characterization of habitat: Savanna[2]	Characterization of habitat: Woodland[3]
Post-1950			Lewis and Rongstad 1992		Krohne *et al.* 1973		
			Hoffmann 1999		Krohne and Schramm 1992		
			Martin *et al.* 2003		Hoffmeister 1989		
			Pergams and Nyberg 2001		Pergams and Nyberg 2001		
	Indiana		Mumford 1969		Johnson and Choromanski-Norris 1992	Mumford and Whitaker 1982	
			Johnson and Choromanski-Norris 1992				
			Lotter 1994				
	Iowa		Bowles 1981	Bowles 1975	Polder 1965		
					Bowles 1981		
	Kansas		Clarke *et al.* 1958		Hall 1955	Brumwell 1951	
			Hall 1955		Platt *et al.* 1973	Cockrum 1952	

		Bee *et al.* 1981			Bee *et al.* 1981
		Platt *et al.* 1973			Andersen and Fleharty 1967
Minnesota	Lewis 1988		Erlien and Tester 1984	Lewis 1988	Gunderson and Beer 1953
					Haggerty 1968
					Robins 1970–1971
					Hazard 1982
Missouri	Ellis 1982	DeSanty-Combes 2002		Ellis 1982	Schwartz and Schwartz 1981
					Ellis 1982
					DeSanty-Combes 2001
Nebraska	Haberman and Fleharty 1971	Jones 1964		Manning and Geluso 1989	Jones 1964
					Haberman and Fleharty 1971
North Dakota					Choromanski-Norris *et al.* 1989
South Dakota				Higgens *et al.* 2000	
Wisconsin		Anthony 1999 Lewis and Rongstad 1992	Jackson 1961		Jackson 1961

[1]=Habitat description includes no mention of woody vegetation, only grasses and forbs.
[2]=Habitat description includes mention of both grassy and woody vegetation.
[3]=Habitat description includes mention of only woody vegetation

Notes

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A Division of the Illinois Department of Natural Resources

ISSN 0073491-8

ILLINOIS
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Review of the New World Erythroneurini (Hemiptera: Cicadellidae: Typhlocybinae)

I. Genera *Erythroneura*, *Erasmoneura*, *Rossmoneura*, and *Hymetta*

Dmitry A. Dmitriev and Christopher H. Dietrich

Illinois Natural History Survey Bulletin
Volume 38, Article 2
August 2007

Illinois Natural History Survey, David L. Thomas, Chief
A Division of the Illinois Department of Natural Resources

Illinois Natural History Survey
Distribution Office
I-Building
1816 South Oak Street
Champaign, IL 61820

Citation:
Review of the New World Erythroneurini (Hemiptera: Cicadellidae: Typhlocybinae). I. Genera *Erythroneura, Erasmoneura, Rossmoneura,* and *Hymetta*. Illinois Natural History Survey Bulletin 38(2):59–128.

Editor: Charles Warwick

US ISSN 0073-4918

US ISBN 1-882932-14-5

Printed by authority of the State of Illinois

Ref. # B382807—.75M—08-07

Printed with soy ink on recycled and recyclable paper.

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Plate1. Photos of Erythroneurini. a – *Erythroneura palimpsesta* McAtee; b – *E. calycula* McAtee; c – *E. acuticephala* Robinson; d – *E. infuscata* Gillette; e – *Erasmoneura vulnerata* Fitch; f – *E. nigra* Gillette; g – *Rossmoneura carbonata* McAtee; h – *Hymetta balteata* McAtee. h – photo by Claude Pilon.

Acknowledgments

For lending specimens, we are grateful to Norman Penny (California Academy of Sciences), K.G.A. Hamilton (Canadian National Collection, Ottawa), Boris Kondratieff (Colorado State University), Richard Brown (Mississippi State University), Stuart McKamey and Warren Steiner (National Museum of Natural History, Washington, D.C.), Luciana Musetti and Creighton Freeman (Ohio State University), and Zachary Falin (University of Kansas). Stuart McKamey kindly provided access to his Leafhoppers of the World Database, which included much of the nomenclatural information incorporated into our Erythroneurini database. Claude Pilon contributed a photo of *Hymetta balteata* McAtee. Unpublished drawings by L.W. Hepner included in this work are used with permission of the Mississippi Entomological Museum. Other previously published drawings reproduced in this work are in the public domain. Irena Dworakowska, Sterling Southern, and Herbert Nickel provided constructive criticism that greatly improved the manuscript. This work was supported in part by NSF grants DEB0315373 and DEB050529679, and Hatch award ILLU-875-361 to CHD.

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CONTENTS

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Dmitry A. Dmitriev and Christopher H. Dietrich

Abstract

This review provides descriptions, illustrations, keys for identification, and summaries of distributions and host plants for all known species of the genera *Erythroneura* (54 species), *Erasmoneura* (12 species), *Rossmoneura* (3 species), and *Hymetta* (5 species). *Erythroneura browni* sp.n., *E. ortha* sp.n., *E. carinata* sp.n., *E. glabra* sp.n., *E. bakeri* sp.n., *E. kerzhneri* sp.n. from Central and Eastern USA, *E. triapitsyni* sp.n. from New Mexico, *Erasmoneura margaritae* sp.n. from Illinois, and *E. emeljanovi* sp.n. from South Carolina are described as new. The following new synonyms are recognized: *Erythroneura prima* Beamer equals *E. maritima* Hamilton syn. n.; *E. diva* McAtee equals *E. tricincta* var. *complementa* McAtee syn. n.; *E. octonotata* Walsh equals *E. comes* var. *compta* McAtee syn. n., *E. cherokee* Robinson syn. n., *E. compta* var. *rufomaculata* McAtee syn. n., and *E. nigroscuta* Johnson syn. n.; *E. cymbium* McAtee equals *E. tricincta* var. *disjuncta* McAtee syn. n.; *E. calycula* McAtee equals *E. tricincta* var. *erasa* McAtee syn. n. and *E. tricincta* var. *noncincta* Johnson syn. n.; *E. ziczac* Walsh equals *E. ziczac* var. *walshi* Beamer syn. n.; *E. delicata* McAtee equals *E. comes* var. *accepta* McAtee syn. n., *E. scripta* Robinson syn. n., and *E. tudella* Robinson syn. n.; *E. rosa* Robinson equals *E. repetita* McAtee, syn. n.; *E. kerzhneri* sp.n. equals *E. vaga* sensu Beamer, 1938 (not Johnson, 1934); *Erasmoneura vulnerata* Fitch equals *E. gradata* Robinson syn. n.; *Erasmoneura fulmina* McAtee equals *E. bicolorata* Beamer syn. n.; *Erasmoneura nigra* Gillette equals *E. vulnerata* var. *decora* McAtee syn. n.; *Erasmoneura nigerrima* McAtee equals *E. atrata* Johnson syn. n.; *Hymetta balteata* McAtee equals *H. trifasciata* var. *albata* McAtee syn. n. and *H. balteata* var. *mediana* Fairbairn syn. n.; *H. anthisma* McAtee equals *H. distincta* Fairbairn syn. n.; *Erasmoneura atra* Johnson, 1935 is restored and equal to *E. nigerrima* sensu Beamer, 1946 (not McAtee, 1920). Neotypes are designated for *Erythroneura octonotata* Walsh, *E. tricincta* Fitch, and *Hymetta trifasciata* Say.

Keywords: Auchenorrhyncha, Homoptera, leafhopper, morphology, phylogeny, taxonomy, USA.

Introduction

The leafhopper tribe Erythroneurini is a diverse group of tiny, delicate leafhoppers that, in the New World, appears to be most diverse in the deciduous forests of temperate North America where species occur on a wide variety of woody host plants. In a recent paper (Dietrich and Dmitriev 2006), we proposed a revised genus-level classification for New World Erythroneurini, recognizing 18 New World genera, including three taxa previously treated as subgenera of *Erythroneura* (sensu lato). Species belonging to five genera restricted to South America, and the small North American genera *Aztegina* Dietrich and Dmitriev, *Hepzygina* Dietrich and Dmitriev, *Illinigina* Dietrich and Dmitriev, *Mexigina* Dietrich and Dmitriev, and *Nelionidia* Dietrich and Dmitriev were treated by Dietrich and Dmitriev (2006). In this and subsequent papers, we provide species-level treatments of the remaining genera of Erythoneurini known to occur in North America. This paper treats the genera *Erythroneura, Erasmoneura, Rossmoneura*, and *Hymetta.* Revisions of the genera *Erythridula*, *Eratoneura*, and *Zyginama* are in preparation.

Taxonomic study of New World Erythroneurini began with Fitch (1851), who described the genus *Erythroneura* based on four species and one variety from New York. Later, Oshanin (1912) designated *E. tricincta* Fitch as the type species. The genus was first revised by McAtee (1920), who described many additional species and varieties, and organized the species into six informal groups based on wing venation. McAtee (1918, 1919, 1920, 1924a, 1924b, 1924c, 1926) recognized species and varieties based on color pattern, usually selecting females as holotypes. Lawson (1920) and Robinson (1926) were the first to recognize the importance of the male genitalia for diagnosing species of *Erythroneura*, and provided the first drawings and descriptions of these structures. However, their keys continued to include only characters of the forewing venation and color pattern. Robinson recognized five groups of species within the genus. In a series of publications, Beamer (1927, 1929, 1930a, 1930b, 1931a, 1931b, 1931c, 1931d, 1932a, 1932b, 1932c, 1932d, 1932e, 1932f, 1932g, 1932h, 1932i, 1937, 1938, 1946) revised *Erythroneura* comprehensively, treating each of four species groups (Beamer 1938) in turn: (Beamer 1930b – *obliqua* group; Beamer 1931a–1932h – *maculata* group; Beamer 1938—*comes* group; Beamer 1946—*vulnerata* group). Beamer provided illustrations of the male genitalia for all known species, incorporated these characters into his keys, and associated males with most of the species and varieties that had been described by McAtee based on females. Johnson (1935) independently revised the species of *Erythroneura* from Ohio and provided a key for their identification. She described many new species in this and subsiquent papers (Knull 1945, 1946, 1951a, 1951b, 1954a, 1954b, 1955). In his generic revision of Western Hemipshere Typhlocybinae, Young (1952) established subgenera for each of Beamer's species groups: *Erythridula, Eratoneura*, *Erythroneura, and Erasmoneura,* respectively, and included these in a new tribe, Erythroneurini, along with two other genera: *Zygina* Fieber and *Hymetta* McAtee (revised by Fairbairn 1928b). After these revisions, H.H. Ross (with D.M. DeLong) and L.W. Hepner described about 300 additional species of *Erythroneura*. Dietrich and Dmitriev (2006) elevated the subgenera to the genus level, and transferred three species of *Erasmoneura* into the new genus *Rossmoneura*.

Species presently included in the four genera treated here are all apparently native to temperate North America, where they feed and oviposit mainly on woody deciduous hosts. A few species of *Erasmoneura* and *Rossmoneura* utilize herbs as hosts for both feeding and oviposition. Adults overwinter in leaf litter. In the spring, they emerge and feed on the new leaves of early emerging deciduous plants before migrating to their "definitive" summer host plants where they mate and lay the eggs (Ross and DeLong 1953). Most species oviposit and undergo nymphal development on a single (or a group of closely related) plant species. In the southern USA, they complete two or more generations per year, but in the North there may be but a single generation. In the fall, adults may again feed on variety host plants prior to seeking out winter shelter. Most New World species of Erythroneurini have no known economic importance, but a few are important pests of grape (McAtee 1920, Robinson 1926, Martinson and Dennehy 1995, Zimmerman et al. 1996, Duso, et al. 2005) and apple (Beamer 1930a).

Material and Methods

Few previous workers have specifically targeted Erythroneurini in their collecting, and specimens from trap catches and other general collecting that find their way into curated collections are often in very poor condition. Because of this, and due to time and budget constraints, this study focused only on collections known to contain large numbers of well-curated specimens of Erythroneurini, as well as those housing primary types: Illinois Natural History Survey (INHS), Ohio State University (OSU), University of Kansas Natural History Museum (KSEM), Mississippi State University, Mississippi Entomological Museum (MEM), Canadian National Collection of Insects, Arachnids and Nematodes (CNC), Smithsonian National Museum of Natural History (USNM), Colorado State University (CSUC), California Academy of Sciences (CAS). The numbers of studied specimens from each collection are summarized in Table 1. Future collecting will undoubtedly show that the distributions of most species are much broader than indicated on the maps accompanying individual species treatments. Although these maps show regional biases reflecting the locations and holdings of the studied collections, they are based on vouchered collection records and, thus, accurately reflect current knowledge of species distributions. The type locality is marked with a star on the maps.

Identification of species was mainly based on type material. In some cases, when the type was not located, or the holotype is a female (e.g., most McAtee's species), we followed Beamer's (1927, 1929, 1930a, 1930b, 1931a, 1931b, 1931c, 1931d, 1932a, 1932b, 1932c, 1932d, 1932e, 1932f, 1932g, 1932h, 1932i, 1937, 1938, 1946) interpretation, based on study of dissected male specimens that he labeled "allotype" to indicate that they had been compared to the female primary types of previous workers. Although Beamer's "allotypes" have no official standing in nomenclature, these dissected male specimens facilitate unambiguous interpretation of Beamer's concept of the species.

Morphological terminology follows Dietrich and Dmitriev (2006). Although individual genera, and in many cases species, have a characteristic color pattern, details and intensity may be highly variable both inter- and intraspecifically. Overwintering individuals tend to be more brightly colored than adults of the summer generation of the same species. This has resulted in many species being described multiple times based on different color forms. Species of *Erythroneura* have the most diverse color patterns. In the descriptions below, the pattern of fully colored individuals is described, although completely or almost completely discolored forms are known for most species. Thus, identification keys are based mainly on male genitalia, with external characters used only for supplemental purposes.

Each species is illustrated by one or more habitus photos taken using a Microptics digital imaging system. Original drawings were prepared only in cases where those available from other sources were deemed inaccurate. Thus, numerous figures are reproduced from other sources, as noted in the figure captions. Inconsistencies (e.g., in line thickness) among line drawings reflect differences in the drawing styles of previous authors. In all cases, figures reproduced from previous publications are either in the public domain or are reproduced with permission.

Line drawings of the male genitalia accompanying each species treatment are labeled as follows:

a – habitus;
b – pygofer or pygofer dorsal appendage, lateral view;
c – style apex, broad aspect;
d – aedeagus, lateral view;
e – aedeagus, ventral view;
f – connective.

Nomenclatural, distributional, morphological and host-plant data summarized below were extracted from a relational specimen-level database of Erythroneurini (Dmitriev & Dietrich, 2003 onwards), developed using the 3I software package (Dmitriev 2006). The online database provides more detailed information for each species, including a complete list of specimens examined, photos of type specimens, and interactive keys to species and genera.

In the species treatments below, only summer host plants are listed, although most species have also been collected from plants other than their oviposition hosts.

To examine the phylogenetic relationships among species, a matrix of 63 morphological characters was compiled for 73 species

of *Erythroneura*, *Erasmoneura* (excluding *E. bipentagona* Beamer), *Rossmoneura*, *Hymetta*, and 13 species from the related genera *Erythridula*, *Eratoneura*, *Illinigina*, and *Neoimbecilla*. *Erythridula* was selected as the outgroup based on results of a previous analysis (Dietrich and Dmitriev 2006). Phylogenetic analysis of this matrix was performed using PAUP* 4.0 (Swofford 1998) with 10,000 random addition sequences (nchuck = 5, chuckscore = 1), and subsequent TBR branch swapping on islands of most parsimonious trees. All multistate characters were treated as non-additive (unordered) except one: Articulation of dorsal pygofer appendage with three ordered states—articulated, not articulated but separated by suture, and fused. Characters were assigned different weights a priori based on their complexity and intraspecific variability. Complex characters that varied little within species were assigned weight = 4; color pattern characters, which are highly variable within some species, were assigned weight = 1; all other characters were assigned weight = 2.

Branch support was measured by calculating the decay index (Bremer 1994) for each consistently resolved node on the most parsimonious trees. This was accomplished using the "enforce topological constraints" option to search for the shortest tree(s) not compatible with each node, using the heuristic search algorithm in PAUP*.

Specimens of newly described taxa are deposited in the insect collections of the Illinois Natural History Survey (Champaign), University of Kansas Natural History Museum (Lawrence), and Mississippi State University (Starkville).

Table 1. Collections and studied material.[1]

#	Species	Museums							
		INHS	OSU	KSEM	MEM	CNC	USNM	CSUC	CAS
1	*Erythroneura kanwakae* Robinson	5	19	33	3	23			
2	*E. fiduciaria* Knull	43	27		2				
3	*E. prima* Beamer			9	1	35			
4	*E. diva* McAtee	6	76	78	53		2		
5	*E. browni* sp.n.	1			51				
6	*E. comes* Say	299	321	65	188	147			
7	*E. octonotata* Walsh	943	266	90	525		1		
8	*E. amanda* McAtee	12	14				1		
9	*E. nudata* McAtee	115	242	81	417	2	1		
10	*E. ortha* sp.n.	1			73				
11	*E. festiva* Beamer	167	57	158	34				
12	*E. gilensis* Beamer	2	46	27	8			2	
13	*E. pontifex* McAtee	126	36	28	7				
14	*E. palimpsesta* McAtee	21	13	8	6				
15	*E. beameri* Robinson	123	207	111	82	4			
16	*E. reflecta* McAtee	143	105	25	15		1		
17	*E. integra* McAtee	11	39	16	62	1	1		
18	*E. carinata* sp.n.	27			25				
19	*E. tricincta* Fitch	17	162	21	32	94			
20	*E. cymbium* McAtee	35	91	55	198		2		
21	*E. calycula* McAtee	54	203	119	292		2		
22	*E. vagabunda* Knull	12	25	1	1				
23	*E. aza* Robinson	16	13	3	17				
24	*E. glabra* sp.n.	3							
25	*E. elegantula* Osborn	173	16	165	22	4			
26	*E. acuticephala* Robinson	20	24	42	27				
27	*E. aclys* McAtee	155	97	67	199		1	3	
28	*E. bistrata* McAtee	130	103	321	431		2		
29	*E. prosata* Johnson	64	24		7				
30	*E. infuscata* Gillette	15	58	68	9		1	1	
31	*E. cancellata* McAtee	109	40	42	6		1		
32	*E. triapitsyni* sp.n.	19							

33	*E. bakeri* sp.n.	12			23				
34	*E. anfracta* Beamer	2	108	85	6	15			
35	*E. ziczac* Walsh	911	163	108	44	183	2		
36	*E. elegans* McAtee	217	370	59	2	5	1	7	
37	*E. delicata* McAtee	212	272	149	38	7	2		
38	*E. vitifex* Fitch	41	321	52	11	56	1	1	
39	*E. rubra* Gillette	63	195	103	46	2	1	2	
40	*E. vitis* Harris	932	424	146	287	212	2		
41	*E. coloradensis* Gillette	225	52	49	22	8	1	6	
42	*E. fraxa* Robinson	49	7	102	54				
43	*E. vaga* Johnson	41	64	1	79				
44	*E. kerzhneri* sp.n.			70	73				
45	*E. kennedyi* Knull		16						
46	*E. ancora* Beamer			3					
47	*E. tacita* Beamer			81	4	1			
48	*E. caetra* McAtee	19	4	141	5	14	1		
49	*E. rosa* Robinson	50	109	104	23	66			
50	*E. omaska* Robinson	244	22	67	74				
51	*E. rubrella* McAtee	987	31	77	26	59	1		
52	*E. corni* Robinson	66	60	155	646	23			
53	*E. bidens* McAtee	38	29	23	16	2	2		
54	*E. ontari* Robinson	19	110	141	11	84			
55	*Erasmoneura vulnerata* Fitch	805	487	76	809	71		5	
56	*E. fulmina* McAtee	20	18	19	3		2		
57	*E. variabilis* Beamer	242	227	404	7	178		2	
58	*E. nigra* Gillette	95	60	161	23	16	2	3	
59	*E. nigerrima* McAtee		14	105			1		
60	*E. atra* Johnson	46	72	22	25				
61	*E. caerula* Beamer		37	28	1				
62	*E. rubricata* Van Duzee	24	8	405				1	1
63	*E. margaritae* sp.n.	17			1				
64	*E. emeljanovi* sp.n.			19					
65	*E. mixta* Beamer		9	188	1				
66	*E. bipentagona* Beamer			1					
67	*Rossmoneura carbonata* McAtee		3	218	6	132			
68	*R. tecta* McAtee	7	37	14	1		1		
69	*R. calva* Beamer			42	1	12			
70	*Hymetta kansasensis* Fairbairn	41	3	9	30				
71	*H. balteata* McAtee	52	164	24	58		2		
72	*H. anthisma* McAtee	27	72	19	1		1		
73	*H. trifasciata* Say	37	41		37				
74	*H. arizoniana* Fairbairn		102	17		1			

[1] The table shows the number of studied specimens from each collection. See "Material and Methods" for the museum abbreviations.

Results

The phylogenetic analysis of morphological data with *a priori* character weighting recovered 2,325 equally parsimonious trees of length 1,119, rescaled consistency index 0.236, and retention index 0.725. The 50% majority rule tree (Plate 2) recovered all included genera as monophyletic, although on some trees *Eratoneura* was paraphyletic with respect to *Erythroneura,* and many relationships within *Erythroneura* were poorly resolved.

Analysis of the same data with all characters having weight = 1 recovered 484 equally parsimonious trees of length 699. Although these trees were 12 steps shorter than the trees obtained in the analysis based on weighted characters (length calculated based on all weights = 1), we prefer the latter estimate because it requires less homoplasy in the characters considered to be more reliable, and the consensus tree resulting from the analysis of equally weighted characters (not shown) was considerably less well resolved.

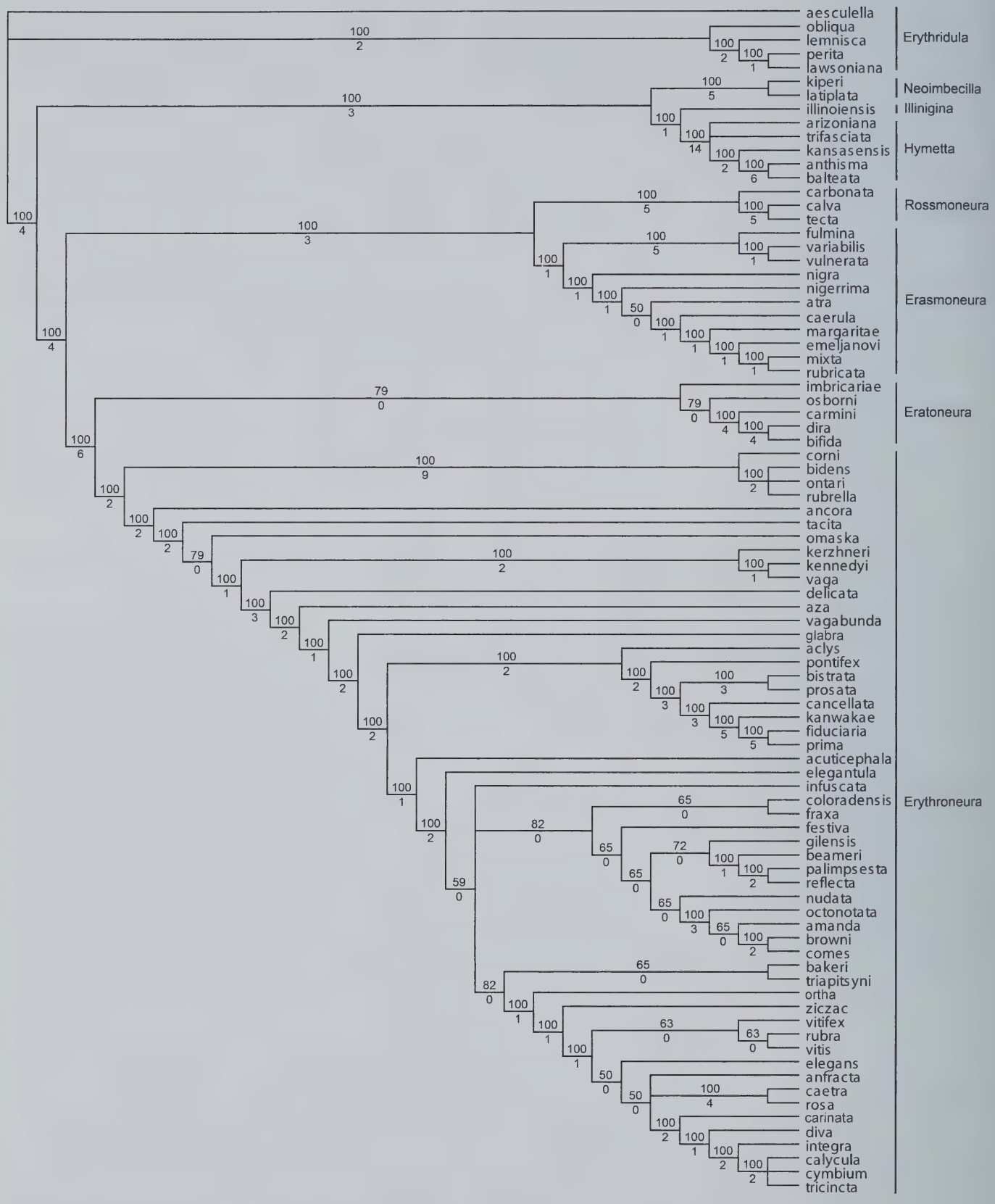


Plate 2. 50% majority rule tree from phylogenetic analysis. Percentage of the trees supporting the node are given above the branches, and decay indices are given below the branches.

Taxonomy

Tribe **Erythroneurini** Young, 1952
Zyginae Zachvatkin, 1946:152, nom.nud.
Erythroneurini Young, 1952:70 (Type: *Erythroneura* Fitch, 1851)
Bakerini Mahmood, 1967:21 (Type: *Bakera* Mahmood, 1967)

Genus ***Erythroneura*** Fitch, 1851
Erythroneura Fitch, 1851:62
Eurythroneura Rathvon, 1869:551, missp.
Erythroneura Oshanin, 1912:114 (Type: *Erythroneura tricincta* Fitch, 1851 designated)
Erthroneura Matsumura, 1932:190, missp.
Erythroueura Lindberg, 1948:161, missp.
Erythroneura (Erythroneura) Young, 1952:79

Description: Length 2.4–3.7 mm, relatively slender. Head narrower than pronotum; crown fore margin strongly produced and angulate medially; ocelli absent or vestigial. Face depressed in profile, less than 45° from horizontal; anteclypeus narrow in both sexes. Forewing outer apical cell about 2X as long as wide or longer; second apical cell quadrate (ir crossvein present); third apical cell parallel sided, straight; CuP longer than segment of CuA between Cu and MP; basal segment of MP longer than basal segment of CuA; inner apical cell with transverse base; Pcu not visible. Hindwing apex broadly rounded or truncate; submarginal vein not extended to wing apex; RA present; MP and CuA fused or separated by m-cu crossvein. Front femur AV row with one basal seta distinctly larger than others; PV row without fine basal setae. Pygofer apex not extended to apex of subgenital plate; dorsal emargination extended to base of segment; dorsolateral internal ridge absent; basolateral setae in distinct group, small; distal setae undifferentiated; sparse long fine setae present; apex with rigid setae on internal surface. Pygofer dorsal appendage immovably fused to margin, without basal suture, bifurcate near base, usually C-shaped, branches widely separated; ventral appendages absent. Subgenital plates free, lateral margin with angulate subbasal projection, section basad of medial constriction shorter than distal section; with four basal macrosetae uniseriate along margin; distinct marginal subbasal small rigid setae forming continuous row. Style preapical lobe prominent; apex usually with three points. Aedeagus articulated to connective; dorsal apodeme broadly expanded in lateral view, usually triangular in ventral view, without sclerotized connection to anal tube or pygofer appendages. Aedeagus with preatrium short or long; shaft symmetrical, in most cases with ventral and/or distal processes. Connective without median anterior lobe; arms long; stem well developed; depressed. Anal tube without processes.

Coloration highly variable among, and in some cases within, species; usually white or yellow overall with orange, reddish, or brownish oblique vittae forming continuous zigzag pattern or broken into separate flecks; crossbands present in some species; forewing often with dark spot on costal margin, near apex of apical cell II, and at base of inner apical cell.

Distribution: Temperate North America; *E. elegantula* Osborn is known from Panama (apparently introduced). Species of *Erythroneura* described from the Old World were listed as *incertae sedis* by Dietrich and Dmitriev (2006) and need to be transferred into other genera.

Host plants: Deciduous trees, shrubs, and vines; most species recorded from *Vitis* spp.

Key to Adult Males of *Erythroneura*

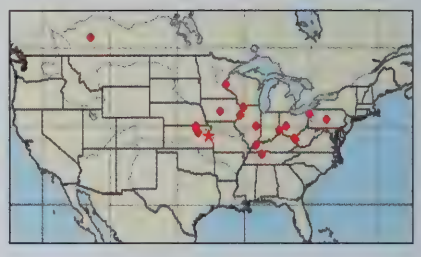
1. Pygofer dorsal appendage three-pointed (ventral branch bifurcate) (Fig. 1b) 2
1'. Pygofer dorsal appendage two-pointed (C-shaped) (Fig. 4b). 4
2(1). Aedeagus ventral processes distally bifurcate (Figs. 2d, 2e). 3
2'. Aedeagus ventral processes not bifurcate, strongly sinuate in lateral view (Figs. 1d, 1e). ..... 1. ***E. kanwakae*** Robinson
3(2). Lateral branch of aedeagus ventral process longer than medial branch (Fig. 2e). Anteclypeus pale. Larger (3.3–3.7 mm). ..... 2. ***E. fiduciaria*** Knull
3'. Lateral branch of aedeagus ventral process shorter than medial branch (Fig. 3e). Anteclypeus dark. Smaller (2.7–3 mm). ..... 3. ***E. prima*** Beamer
4(1). Aedeagus with ventral processes (Figs. 4d, 4e). 5
4'. Aedeagus without ventral processes (Figs. 52d, 52e). 52
5(4). Aedeagus ventral processes as long as shaft or longer (Figs. 4d, 4e). 6
5'. Aedeagus ventral processes shorter than shaft (Fig. 46d). 46
6(5). Aedeagus ventral processes bifurcated or with preapical projection (Figs. 6d1, 7d). 7
6'. Aedeagus ventral processes simple (Fig. 10d). 11
7(6). Aedeagus ventral process with short preapical projection (Fig. 6d1). 8
7'. Aedeagus ventral process with two long branches subequal in length (Fig. 7d). 10
8(7). Third point of style apex shorter than distance between other two points (Fig. 4c). Forewing with narrow red crossband (Fig. 4a). ..... 4. ***E. diva*** McAtee
8'. Third point of style apex longer than distance between other two points (Fig. 6c). Forewing without crossband. 9
9(8). Apex of aedeagus extended well beyond bases of distal processes, with distinct spicules (Fig. 5e). ..... 5. ***E. browni*** sp.n
9'. Apex of aedeagus not extended beyond bases of distal processes, without spicules (Fig. 6e). ..... 6. ***E. comes*** Say
10(7). Aedeagus ventral processes bifurcate close to base (Fig. 7d). Clavus with black spot (Fig. 7a). ..... 7. ***E. octonotata*** Walsh
10'. Aedeagus ventral processes bifurcate more distad from base (Fig. 8d). Clavus without black spot; forewing with broad red crossband (Fig. 8a). ..... 8. ***E. amanda*** McAtee
11(6). Third point of style apex elongate, about as long or longer than distance between other two points (Fig. 16c). 12
11'. Third point of style apex shorter than distance between other two points (Fig. 19c). 21
12(11). Aedeagus ventral processes nearly parallel to each other (Fig. 9e). 13
12'. Aedeagus ventral processes strongly divergent apically (Fig. 16e). 15
13(12). Aedeagus ventral processes strongly sinuate in lateral view (Fig. 9d). ..... 9. ***E. nudata*** McAtee
13'. Aedeagus ventral processes straight or only slightly sinuate in lateral view (Fig. 10d). 14
14(13). Apex of aedeagus extended well beyond bases of distal processes, compressed, with distinct apical spicules. Aedeagus distal processes strongly divergent in ventral view (Fig. 10e). Anteclypeus pale. ..... 10. ***E. ortha*** sp.n.
14'. Apex of aedeagus extended little beyond bases of distal processes, rounded in crossection, without spicules. Aedeagus distal processes parallel in ventral view (Fig. 11e). Anteclypeus dark. ..... 11. ***E. festiva*** Beamer
15(12). Apex of aedeagus extended well beyond bases of distal processes (Fig. 11e). 16
15'. Apex of aedeagus extended little if any beyond bases of distal processes (Fig. 16e). 18
16(15). Shaft of aedeagus denticulate distally (Figs, 5d, 5e). ..... 5. ***E. browni*** sp.n
16'. Shaft of aedeagus smooth (Figs. 12d, 12e). 17
17(16). Aedeagus ventral processes curved dorsad distally in lateral view (Fig. 12d). Vertex with orange pattern (Fig. 12a). ..... 12. ***E. gilensis*** Beamer
17'. Aedeagus ventral processes curved ventrad distally in lateral view (Fig. 13d). Vertex usually black (Fig. 13a). ..... 13. ***E. pontifex*** McAtee
18(15). Aedeagus distal processes only slightly divergent distally in ventral view (Fig. 14e); dorsal carina not reaching apex (Fig. 14d). ..... 14. ***E. palimpsesta*** McAtee
18'. Aedeagus distal processes strongly divergent distally in ventral view (Fig. 16e); dorsal carina reaching apex (Fig. 16d). 19

19(18). Aedeagus ventral processes abruptly bent laterad 90° distally in ventral view (Fig. 15e), sinuate distally in lateral view (Fig. 15d); shaft without distal vestiture..... ..... 15. ***E. beameri*** Robinson
19'. Aedeagus ventral processes evenly curved distally in ventral view (Fig. 16e), straight or curved ventrally in lateral view (Fig. 16d); shaft with distal vestiture. 20
20(19). Aedeagus ventral processes strongly compressed basally (Figs. 16d, 16e). Forewing with oblique vittae forming continuous zigzag pattern (Fig. 16a). .....16. **E. reflecta** McAtee
20'. Aedeagus ventral processes only slightly compressed (Figs. 17d, 17e). Forewing with broken oblique vittae (Fig. 17a). ..... 6. **E. comes** Say
21(11). Forewing with narrow crossband (rarely incomplete) near midlength, apex dark, base pale; mesonotum dark (at least lateral triangles) (Figs. 17a, 20a). 22
21'. Color pattern not as above. 26
22(21). Ventral branch of pygofer dorsal appendage much longer than dorsal branch (Fig. 17b). ..... 17. **E. integra** McAtee
22'. Branches of pygofer dorsal appendage of subequal length (Fig. 18b). 23
23(22). Aedeagus with strong dorsal keel, apex extended well beyond bases of distal processes (Figs. 18d, 18e). ..... 18. **E. carinata** sp.n.
23'. Aedeagus without dorsal keel, apex extended little if any beyond bases of distal processes (Figs. 20d, 20e). 24
24(23). Aedeagus ventral processes strongly sinuate in lateral view, with apices curved dorsad (Fig. 19d). ..... 19. **E. tricincta** Fitch
24'. Aedeagus ventral processes straight or with apices curved ventrad (Fig. 20d). 25
25(24). Aedeagus distal processes more slender, their apices more distal in lateral view (Fig. 20d). ..... 20. **E. cymbium** McAtee
25'. Aedeagus distal processes broader, their apices more basal in lateral view (Fig. 21d). .... 21. **E. calycula** McAtee
26(21). Third point of style apex subequal to or longer than half distance between other two points (Fig. 22c). 27
26'. Third point of style apex shorter than half distance between other two points (Fig. 32c). 34
27(26). Aedeagus distal processes slender (Figs. 22d, 22e). 28
27'. Aedeagus distal processes broad (Figs. 25d, 25e). 30
28(27). Aedeagus ventral processes evenly divergent (Fig. 22e). ..... 22. **E. vagabunda** Knull
28'. Aedeagus ventral processes parallel to each other on ventral side of aedeagus (Fig. 24e). ... 29
29(28). Shaft of aedeagus straight in lateral view, with dorsal distal lobe (Fig. 23d). ....23. **E. aza** Robinson
29'. Shaft of aedeagus curved dorsally, without dorsal distal lobe (Fig. 24d). .... 24. **E. glabra** sp.n.
30(27). Aedeagus ventral processes parallel or slightly divergent in ventral view (Figs. 25e, 26e). Pronotum usually pale with Y-shaped orange vita medially (Fig. 26a). 31
30'. Aedeagus ventral processes strongly divergent apically in ventral view (Figs. 27e, 28e). Pronotum mostly dark brown (Figs. 27a, 28a). 32
31(30). Apex of aedeagus extended beyond bases of distal processes (Fig. 25e). Mesonotum with black basal triangles (Fig. 25a). ..... 25. **E. elegantula** Osborn
31'. Apex of aedeagus not extended beyond bases of distal processes (Fig. 26e). Mesonotum without black basal triangles (Fig. 26a). ..... 26. **E. acuticephala** Robinson
32(30). Aedeagus distal processes each with two sharp points, falcate distally in ventral view (Figs. 27d, 27e). Lateral margins of pronotum pale contrasting with dark brown medial area (Fig. 27a). ..... 27. **E. aclys** McAtee
32'. Aedeagus distal processes each with one sharp point, diamond-shaped in ventral view (Figs. 28d, 28e). Lateral margins of pronotum usually dark, concolorous with medial area (Figs. 28a, 29a). 33
33(32). Scutellum pale. Forewing often with crossbands (Fig. 28a). ..... 28. **E. bistrata** McAtee
33'. Scutellum dark. Forewings without crossbands (Fig. 29a). ..... 29. **E. prosata** Johnson
34(26). Dorsum almost completely black (Fig. 30a). ..... 30. **E. infuscata** Gillette

34'. Ground color of dorsum various, but not black. 3
35(34). Aedeagus ventral processes strongly divergent apically (Fig. 32e). 3
35'. Aedeagus ventral processes not or only slightly divergent apically (Fig. 36e). 3
36(35). Dorsal branch of pygofer dorsal appendage about half length of ventral branch (Fig. 31b). Aedeagus distal processes rounded in ventral view (Fig. 31e). Forewings with pale diamond-shaped transcommisural marking outlined with dark brown (Fig. 31a). ..... 31. **E. cancellata** McAte
36'. Branches of pygofer dorsal appendage subequal in length (Fig. 32b). Aedeagus distal processes pointed in ventral view (Fig. 32e). Forewings with broken oblique vitae (Figs. 32a, 33a). 3
37(36). Aedeagus ventral processes narrowing distally in lateral view (Fig. 32d). Mesonotum with black lateral triangles (Fig. 32a). ..... 32. **E. triapitsyni** sp.n
37'. Aedeagus ventral processes of even width in lateral view (Fig. 33d). Mesonotum without black triangles (Fig. 33a). ..... 33. **E. bakeri** sp.n
38(35). Aedeagus apex extended beyond bases of distal processes (Fig. 36e). 3
38'. Aedeagus apex not extended beyond bases of aedeagus distal processes (Fig. 40e). 4
39(38). Aedeagus compressed, with strong dorsal keel (Fig. 34d). 4
39'. Aedeagus rounded in crossection, dorsal carina if present, feebly developed (Fig. 38d). 4
40(39). Aedeagus ventral processes strongly sinuate in lateral view (Fig. 34d). ..... 34. **E. anfracta** Beame
40'. Aedeagus ventral processes straight in lateral view (Fig. 36d). 4
41(40). Shaft of aedeagus in ventral view extended more than twice its width beyond bases of distal processes (Fig. 35e). Forewings with continuous zigzag pattern (Fig. 35a). ..... 35. **E. ziczac** Walsh
41'. Shaft of aedeagus in ventral view not extended more than twice its width beyond bases of distal processes (Fig. 36e). Forewings with crossbands interrupted with red longitudinal veins (Fig. 36a). ..... 36. **E. elegans** McAtee
42(39). Aedeagus with distal processes slender (Fig. 37d); apex of shaft beyond distal processes slightly broadened (Fig. 37e). ..... 37. **E. delicata** McAtee
42'. Aedeagus with distal processes flattened (Fig. 38d); apex of shaft beyond distal processes not broadened (Fig. 38e). 43
43(42). Second point of style apex longer than third (Fig. 38c). Aedeagus ventral processes convergent distally (Fig. 38e). ..... 38. **E. vitifex** Fitch
43'. Second point of style apex shorter than third (Fig. 39c). Aedeagus ventral processes divergent distally (Fig. 39e). ..... 39. **E. rubra** Gillette
44(38). Second point of style apex longer than third (Fig. 40c). Forewing mostly dark with two pale narrow crossbands, sometimes interrupted with red longitudinal veins (Fig. 40a). ..... 40. **E. vitis** Harris
44'. Second point of style apex as short or shorter than third (Fig. 42c). Forewing without crossbands (Figs. 41a, 42a). 45
45(44). Aedeagus distal processes broadened distally in ventral view (Fig. 41e). Mesonotum with black lateral triangles. Forewing with broken oblique vittae (Fig. 41a). ..... 41. **E. coloradensis** Gillette
45'. Aedeagus distal processes diamond-shaped in ventral view (Fig. 42e). Mesonotum with red lateral triangles. Forewing with continuous zigzag pattern (Fig. 42a). ..... 42. **E. fraxa** Robinson
46(5). Aedeagus with dorsal processes placed on phallobase or between phallobase and shaft of aedeagus (Figs. 43d, 45d). 47
46'. Aedeagus without dorsal processes (Fig. 46d). 49
47(46). Aedeagus with unpaired small dorsal process on phallobase (Fig. 43d). ..... 43. **E. vaga** Johnson
47'. Aedeagus with pair of long dorsal processes between aedeagus shaft and phallobase (Figs. 45d, 45e). 48
48(47). Third point of style apex longer than distance between other two points (Fig. 44c). Aedeagus distal processes shorter (Figs. 44d, 44e). ..... 44. **E. kerzhneri** sp.n.
48'. Third point of style apex shorter than distance between other two points (Fig. 45c). Aedeagus distal processes longer (Figs. 45d, 45e). ..... 45. **E. kennedyi** Knull
49(46). Aedeagus ventral processes placed close to shaft (Fig. 46d). Dorsal branch of pygofer dorsal appendage subequal to ventral branch (Fig. 46b). ..... 46. **E. ancora** Beamer

49'. Aedeagus ventral processes well separated from shaft (Fig. 47d). Dorsal branch of pygofer dorsal appendage much shorter than ventral branch (Fig. 47b). 50
50(49). Aedeagus ventral processes divergent (Fig. 47e). ..... 47. **E. tacita** Beamer
50'. Aedeagus ventral processes parallel to each other (Fig. 48e). 51
51(50). Branches of pygofer dorsal appendages convergent distally in lateral view, ventral branch distally slightly curved upward (Fig. 48b). Aedeagus in ventral view broadened preapically (Fig. 48e). ..... 48. **E. caetra** McAtee
51'. Branches of pygofer dorsal appendages strongly divergent in lateral view (Fig. 49b). Aedeagus in ventral view not broadened preapically (Fig. 49e). ..... 49. **E. rosa** Robinson
52(4). Aedeagus with pair of large distal processes and pair of smaller preapical processes (Figs. 50d, 50e). Pygofer dorsal appendages short (Fig. 50b). ..... 50. **E. omaska** Robinson
52'. Aedeagus without distal and preapical processes (Figs. 52d, 52e). Pygofer dorsal appendage long (Fig. 52b, 53b). 53
53(52). Aedeagus broad in ventral view, with strong dorsal keel (Figs. 51d, 51e). ..... 51. **E. rubrella** McAtee
53'. Aedeagus slender in ventral view, without dorsal keel, with dorsal distal lobe (Figs. 52d, 52e). 54
54(53). Dorsal branch of pygofer dorsal appendage subequal to ventral branch (Fig. 52b). ..... 52. **E. corni** Robinson
54'. Dorsal branch of pygofer dorsal appendage much shorter than ventral branch (Fig. 53b). ... 55
55(54). Ventral branch of pygofer dorsal process sinuate in lateral view (Fig. 53b). Larger (2.8–3.2 mm). ..... 53. **E. bidens** McAtee
55'. Ventral branch of pygofer dorsal process evenly curved upward (Fig. 54b). Smaller (2.5–2.8 mm). ..... 54. **E. ontari** Robinson

1. ***Erythroneura kanwakae*** Robinson, 1924 (Fig. 1)
Erythroneura kanwakae Robinson, 1924c:292



Description. Length 2.9–3.1 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe angulate apically; dorsal appendages three-pointed (ventral branch bifurcated), extended beyond pygofer apex. Second point of style apex well developed, third point shorter than second. Aedeagus with preatrium longer than shaft; shaft curved dorsally, slender in lateral view, depressed in crossection; apex broadened in ventral view, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at apex; distal processes apical, flattened, directed dorsad. Dorsum yellow or white, with red or brownish color pattern; vertex with orange parallel submedial lines (often with lateral branch), midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum entirely pale; thoracic venter with dark mesosternum, remainder pale; forewing with oblique vittae forming continuous zigzag pattern; clavus with separate basal and distal vittae; dark spots at costal margin; apical cell II without distal spot; inner apical cell without brown spot.
Type locality: Holotype ♂, USA, Kansas, Douglas Co., IV 1924, (Robinson), (KSEM).
Distribution: Central and northeastern USA, southern Canada.
Host plants: *Ribes hirtellum*.

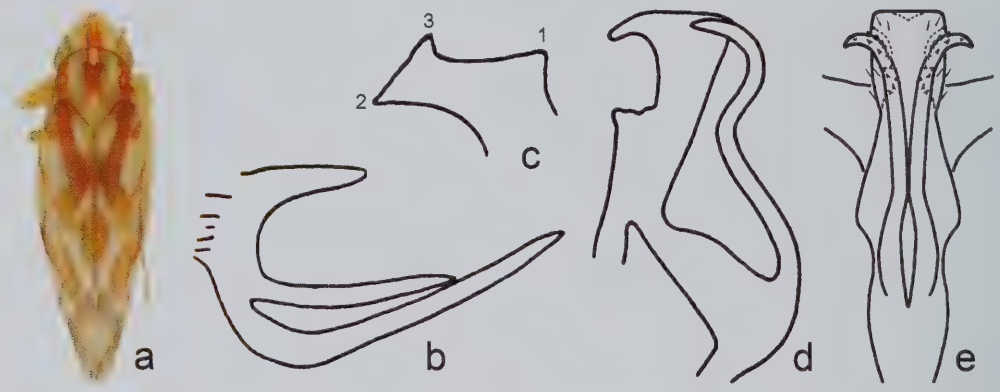
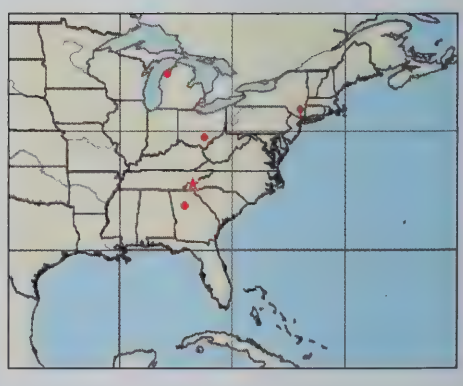


Figure 1. *E. kanwakae* Robinson. b, d – from Beamer 1938; c – from Hepner, unpublished.

2. ***Erythroneura fiduciaria*** Knull, 1951 (Fig. 2)
Erythroneura fiduciaria Knull, 1951a:170



Description: Length 3.3–3.7 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe angulate; dorsal appendages three-pointed (ventral branch bifurcated), extended beyond pygofer apex. Second point of style apex longer than third, third point very short. Aedeagus with preatrium longer than shaft; shaft curved dorsally, slender in lateral view, round in crossection; with ventral processes placed basally, well separated from shaft, longer than shaft, divergent at apex, bifurcated, with lateral branch longer than medial one; distal processes apical, triangular. Dorsum yellow or white, with reddish-brown color pattern; vertex with orange parallel submedial lines with lateral branch, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum entirely pale; thoracic venter with dark mesosternum, remainder pale; forewing with oblique vittae forming continuous zigzag pattern; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.
Type locality: Holotype ♀, USA, Tennessee, Sevier Co., Great Smoky Mountain National Park, 21 VI 1942 (Knull), (OSU).

Distribution: Eastern USA.
Host plants: *Hamamelis virginiana, H. macrophylla.*

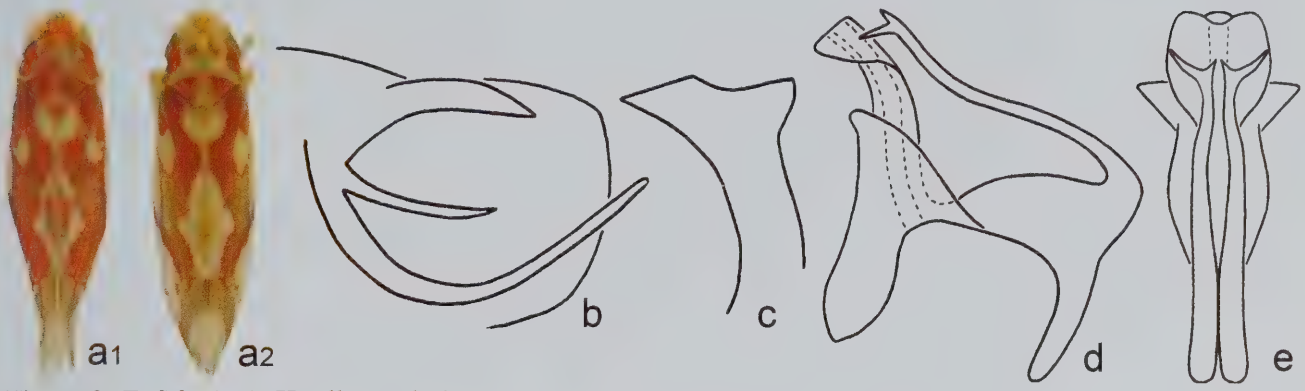
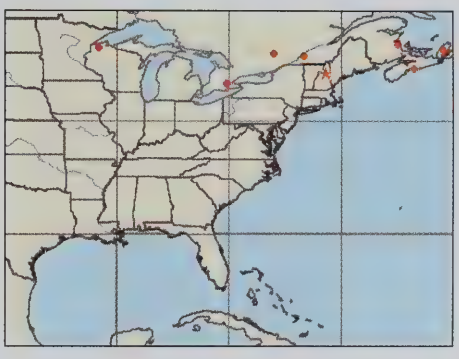


Figure 2. *E. fiduciaria* Knull. a1 – holotype; a2 – color variation.

3. ***Erythroneura prima*** Beamer, 1938 (Fig. 3)
Erythroneura prima Beamer, 1938:264
Erythroneura maritima Hamilton, 1987 in Hamilton & Langor, 1987:679 **syn.n.**



Description: Length 2.7–3 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded, dorsal appendages 3 pointed (ventral branch bifurcated), extended beyond pygofer apex. Second point of style apex longer than third; third point very short. Aedeagus with preatrium longer than shaft; shaft curved dorsally, slender in lateral view, round in crossection; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at apex, with small preapical tooth; distal processes apical, triangular. Dorsum yellow or white, with reddish or brownish color pattern; vertex with orange parallel submedial lines (often with lateral branch), midline pale; anteclypeus brown; pronotum almost entirely dark; mesonotum pale, with dark lateral triangles; thoracic venter entirely dark; forewings with oblique vittae forming continuous zigzag pattern; clavus largely or entirely bright red or brownish; dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.
Type locality: Holotype ♂, USA, New Hampshire, Coos Co., Bretton Woods, 31 VIII 1934 (Beamer), (KSEM).
Distribution: North-central and northeastern USA, southeastern Canada.
Host plants: Unknown.

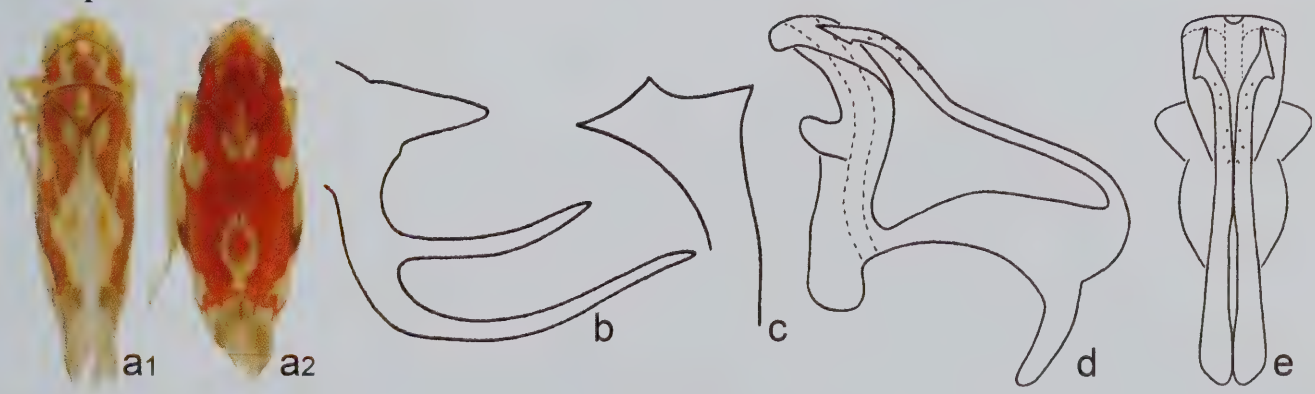
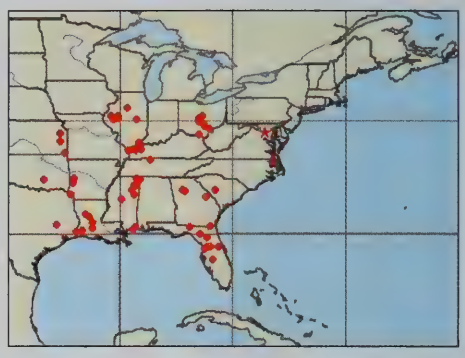


Figure 3. *E. prima* Beamer. a2 – var. *maritima*. b – from Beamer 1938.

4. ***Erythroneura diva*** McAtee, 1920 (Fig. 4)
Erythroneura tricincta var. *diva* McAtee, 1920:308
Erythroneura tricincta var. *rubravitta* Robinson, 1924b:156
Erythroneura tricincta var. *complementa* McAtee, 1926:135 **syn.n.**
Erythroneura diva Beamer, 1938:269



Description: Length 3–3.2 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendage not extended beyond pygofer apex, C-shaped, branches of subequal length. Second point of style apex longer than third; third point short; angle between basal and third points about 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, broad in lateral view, round in crossection, with dorsal carina, and distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus, with small preapical tooth; distal processes subapical, triangular. Dorsum yellow or white; anteclypeus pale, concolorous with rest of face; pronotum almost entirely red; coloration of mesonotum vary from entirely pale to dark, scutellum pale; thoracic venter entirely pale; forewing without (rarely with) oblique vittae, with red narrow crossband near midlength and darkened apex; dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.
Type locality: Holotype ♀, USA, Maryland, Montgomery Co., Plummers Island, 26 VII 1914 (McAtee), (USNM).
Distribution: Central and eastern USA.
Host plants: *Vitis* spp.

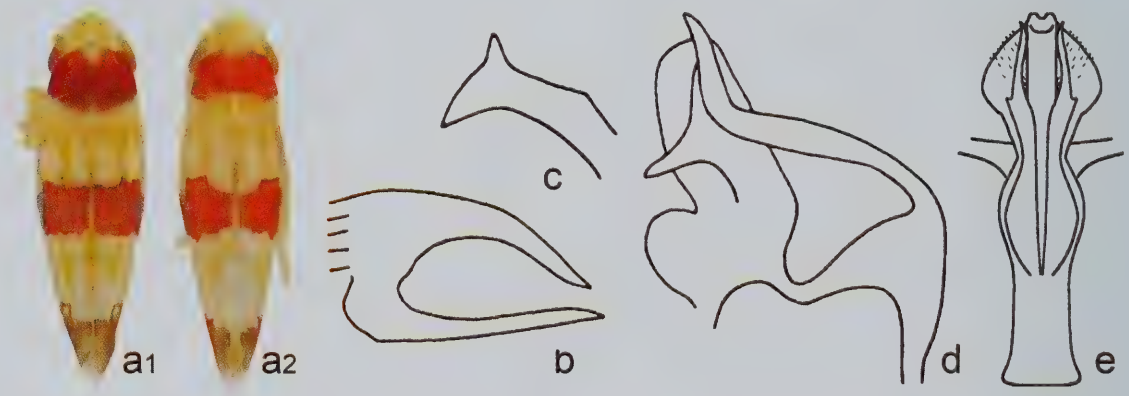
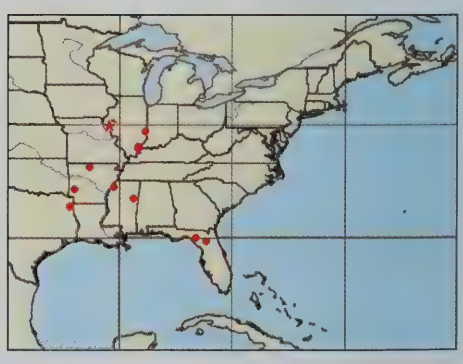


Figure 4. *E. diva* McAtee. a2 – var. *complementa*. b–d — from Beamer 1938.

5. ***Erythroneura browni*** Dmitriev & Dietrich **sp.n.** (Fig. 5)



Description: Length 2.7–3 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendage not extended beyond pygofer apex, C-shaped, branches subequal in size. Second point of style apex very short, tooth like; third point elongate, longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft straight and slender in lateral view, denticulate distally, round in crossection, strongly extended beyond bases of distal processes, often with distal lobe strongly varying in length; apex truncate in posterior view, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at apex, often with small tooth near midlength; distal processes long, flattened, triangular. Coloration similar to that of *E. comes* Say. Dorsum yellow or white with orange color pattern; vertex with orange parallel submedial lines with lateral branch, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with

Y- shaped medial vitta; mesonotum entirely pale; thoracic venter entirely pale; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.

Diagnosis: *E. browni* sp.n. is similar to *E. comes* Say, but shaft of aedeagus extends well beyond the bases of the distal processes and is denticulate. It is also similar to *E. ortha* sp.n., but the aedeagus lacks a dorsal keel and has the ventral processes divergent apically.

Type locality: Holotype ♂, USA, Illinois, Brown Co., Siloam Springs, 19 IV 1960 (Ross & Cunningham), (INHS).

Studied material: Paratypes: 1 ♂, Arkansas, Marion Co., Yellville, 23 VIII 1962 (Hepner), (MEM); 4 ♂, Florida, Alachua Co., Gainesville, 30 VI–2 X 1970–1972 (Mead); 1 ♂, Florida, Lafayette Co., on *Vitis sp.*, 1 VIII 1956 (Mead); 5 ♂, Illinois, Brown Co., Siloam Springs, (Ross & Cunningham); 8 ♂, Illinois, Brown Co., Siloam Springs, 29 IV 1960 (Ross & Cunningham); 1 ♂, Mississippi, Oktibbeha Co., State College, 4 III 1968 (Hepner), (MEM); 1 ♂ Texas, Marion Co., Jefferson, 3 VII 1962 (Hepner), (MEM); other studied material from Illinois, Arkansas, Mississippi excluded from type series.

Distribution: Central and southeastern USA.

Host plants: *Vitis* spp.

Note: This species is named in honor of Prof. Richard L. Brown, Director of the Mississippi Entomological Museum, who graciously loaned us the museum's entire *Erythroneura* collection and provided access to Leon Hepner's unpublished manuscripts, rearing records, notes, and illustrations.

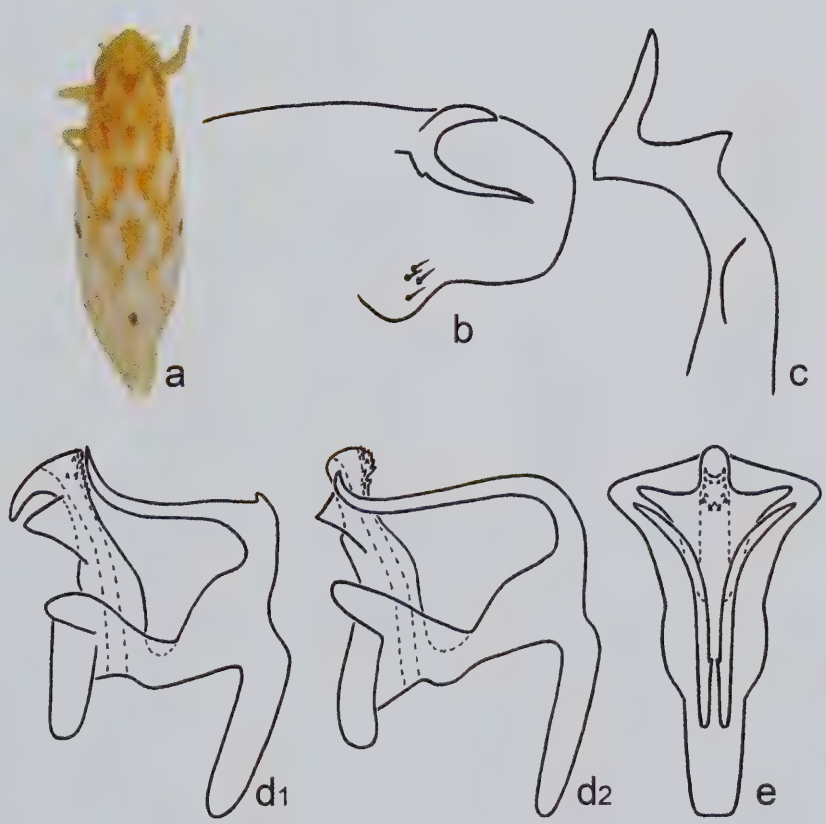
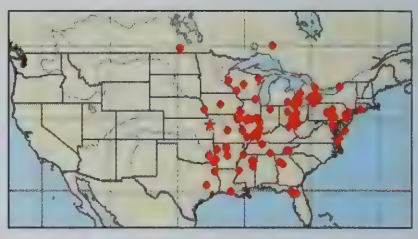


Figure 5. *E. browni* sp.n. d_1, d_2 – *aedeagus* variation.

6. ***Erythroneura comes*** (Say, 1825) (Fig. 6)
Tettigonia comes Say, 1825:343
Erythroneura comes Smith, 1890:447
Typhlocyba comes comes Gillette, 1898:764
Erythroneura comes Beamer, 1938:292, neotype designation
Eastern grape leafhopper



Description: Length 2.7–3 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches of subequal length. Second point of style apex very short, tooth like; third point elongate, longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, broad in lateral view; round in crossection; with dorsal carina, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft; divergent at apex, often with small tooth near midlength; distal processes apical, triangular. Dorsum yellow or white with orange color pattern; vertex with orange parallel submedial lines with lateral branch, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y- or V-shaped medial vitta; mesonotum entirely pale; thoracic venter entirely pale; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Neotype ♂, USA, Kansas, Leavenworth Co., 11 IV 1930 (Beamer), (KSEM).
Distribution: Central and eastern USA, southeastern Canada.
Host plants: *Vitis* spp.

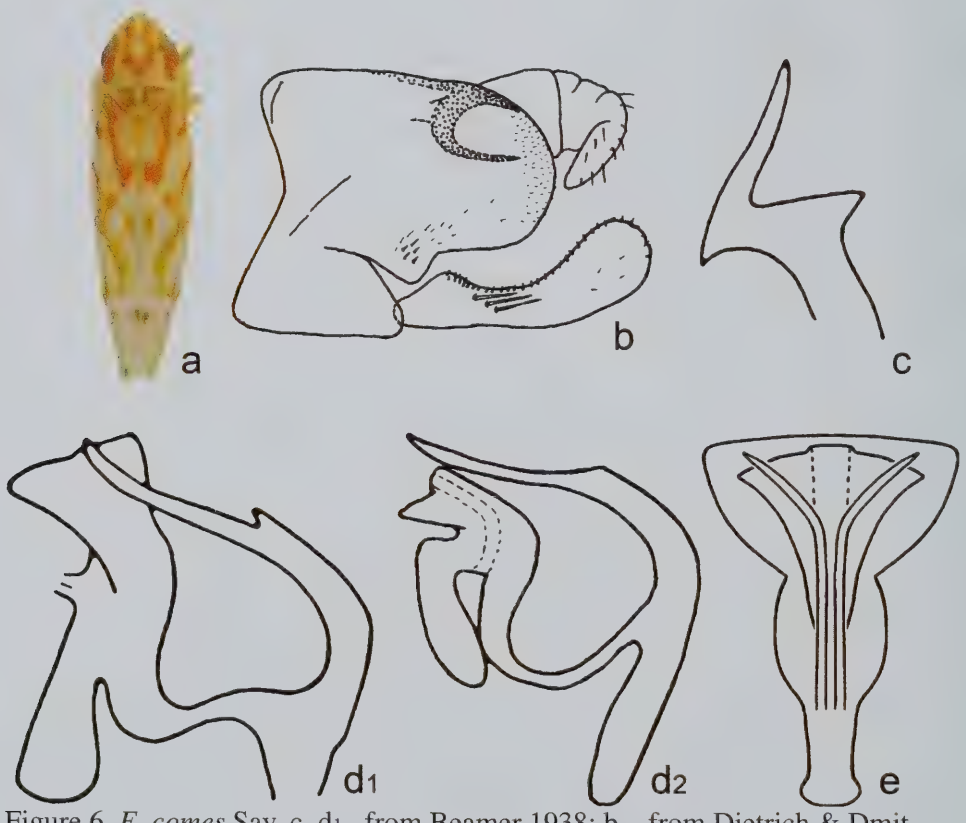
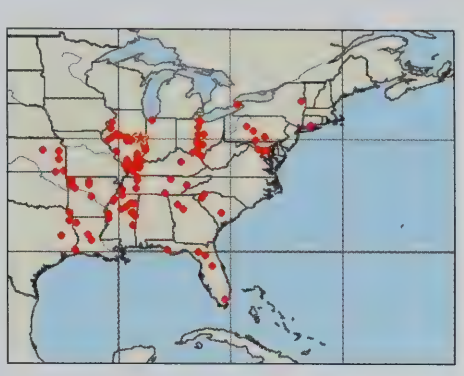


Figure 6. *E. comes* Say. c, d_1 –from Beamer 1938; b – from Dietrich & Dmitriev 2006; d_2 – from Hepner, unpublished.

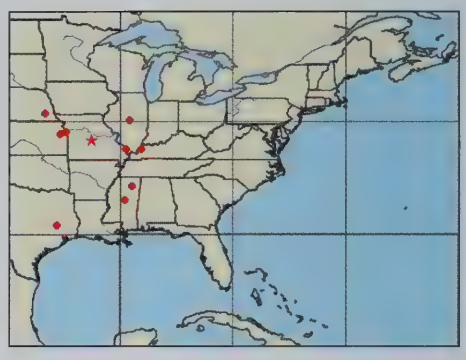
7. ***Erythroneura octonotata*** Walsh, 1862 (Fig. 7)
Erythroneura octo-notata Walsh, 1862:149
Erythroneura comes var. *compta* McAtee, 1920:318 **syn.n.**
Erythroneura octolineata Lawson, 1922:336 missp.
Erythroneura cherokee Robinson, 1924b:154 **syn.n.**
Erythroneura compta var. *rufomaculata* McAtee, 1924c:43 **syn.n.**
Erythroneura nigroscuta Johnson, 1934: 258 **syn.n.**
Erythroneura rufromaculata Oman, 1949:95 missp.



Description: Length 2.6–2.9 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches of subequal length. Second point of style apex very short, tooth like; third point elongate, longer than distance between other two points; angle between basal and third point of style less than 90°. Aedeagus with preatrium longer than shaft; shaft stright and broad in lateral view, round in crossection, with dorsal carina, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, bifurcated close to base; distal processes subapical, triangular. Dorsum yellow or white, with orange color pattern; coloration strongly varies; vertex unicolorous or with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y- or V-shaped medial vitta; mesonotum pale, usually with dark brown medial spot; thoracic venter entirely pale; forewing without oblique vittae or with broken oblique vittae; clavus with separate basal and distal vittae and dark brown spot near midlength, sometimes basal vitta bright red; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Neotype ♂, USA, Illinois, Champaign Co., St. Joseph, 3 IX 1916, (INHS) – here designated.
Distribution: Central and eastern USA.
Host plants: *Vitis* spp.
Note: The holotype, along with the rest of Walsh's collection, was destroyed in the Chicago fire of 1871. A neotype is here designated to fix the identity of the species.

Figure 7. *E. octonotata* Walsh. a2 – var. *compta*; a3 – var. *rufomaculata;* a4 – var. *nigroscuta*. b, e –from Beamer 1938; c, d – from Hepner, unpublished.

8. ***Erythroneura amanda*** McAtee, 1920 (Fig. 8)
Erythroneura comes var. *amanda* McAtee, 1920:319
Erythroneura amanda Robinson, 1926:137



Description: Length 2.4–2.6 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches of subequal length. Second point of style apex very short, tooth like; third point elongate, about as long or longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft straight and broad in lateral view, compressed in crossection, with dorsal carina; ventral processes placed basally, well separated from shaft, longer than shaft, bifurcate near midlength, divergent at apex; distal processes subapical, triangular. Dorsum yellow or white; color pattern red and orange; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum almost entirely dark; thoracic venter entirely pale; forewing with broken oblique vittae and wide red crossband at base; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype ♂, USA, Missouri, VII, on *Vitis* spp., (USNM).
Distribution: Central and southeastern USA.
Host plants: *Vitis* spp.

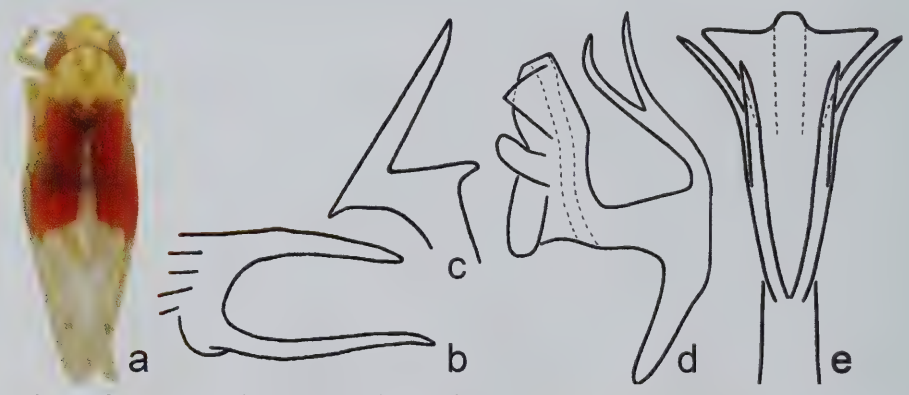
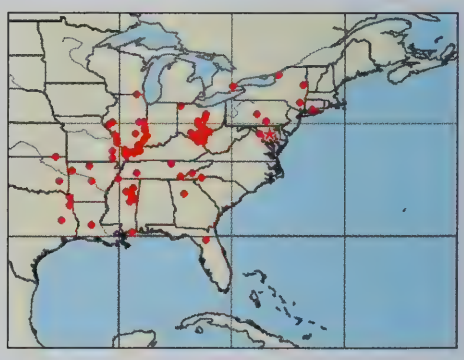


Figure 8. *E. amanda* McAtee. b, c – from Beamer 1938.

9. ***Erythroneura nudata*** McAtee, 1920 (Fig. 9)
Erythroneura comes var. *nudata* McAtee, 1920:316
Erythroneura attenuata Johnson, 1934:260
Erythroneura nudata Beamer 1938:284



Description: Length 2.8–3.1 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches of subequal length. Second point of style apex very short, tooth like; third point elongate, longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft straight and broad in lateral view, depressed in crossection, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes apical or subapical, triangular. Coloration similar to that of *E. comes* Say.
Type locality: Holotype ♂, USA, Maryland, Anne Arundel Co., Odenton, 26 VII 1914 (McAtee), (USNM).
Distribution: Central and eastern USA, southeastern Canada.
Host plants: *Vitis* spp.

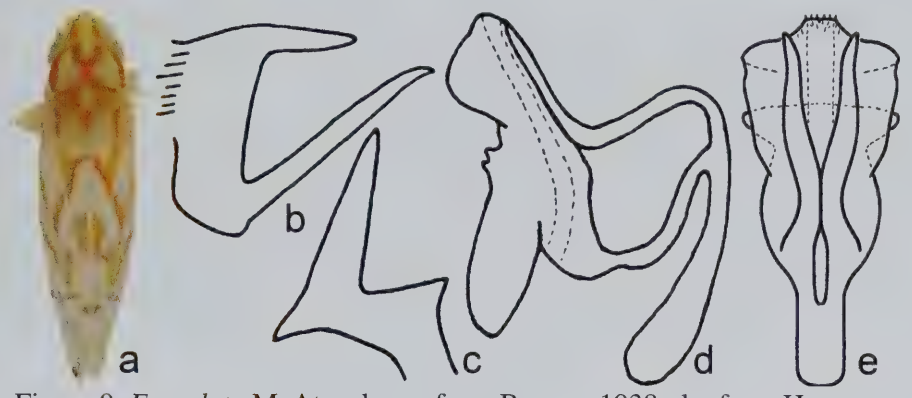
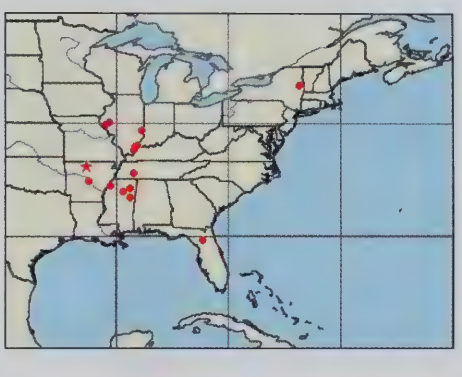


Figure 9. *E. nudata* McAtee. b, c – from Beamer 1938; d – from Hepner, unpublished.

10. ***Erythroneura ortha*** Dmitriev & Dietrich **sp.n.** (Fig. 10)



Description: Length 2.8–3 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended to pygofer apex, C-shaped, branches of subequal size. Second point of style apex very short, tooth like; third point elongate, longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, broad in lateral view, compressed in crossection, with dorsal carina and distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes subapical, flattened, triangular. Coloration similar to that of *E. comes* Say; dorsum yellow or white with orange color pattern; vertex with orange parallel submedial lines (often with lateral branch), midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y- or V-shaped medial vitta; mesonotum entirely pale; thoracic venter entirely pale; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.

Diagnosis: *E. ortha* sp.n. is similar to *E. comes* Say and *E. gilensis* Beamer, but the shaft of the aedeagus is produced well beyond the bases of the distal processes; and the ventral processes are parallel to each other on the ventral side of the aedeagus. It also differs from *E. comes* Say in having the shaft of aedeagus compressed with a strong dorsal keel.

Type locality: Holotype ♂, USA, Arkansas, Marion Co., Yellville, on *Cercis canadensis*, 23 VIII 1962 (Hepner), (INHS).

Studied material: Paratypes: 28 ♂, Arkansas, Marion Co., Yellville, on *Cornus* sp., *Cercis canadensis, Acer* sp., *Vitis* sp., 23 VIII 1962 (Hepner) (MEM). Other studied material from Florida, Illinois, Mississippi, New York, and Tennessee excluded from type series.

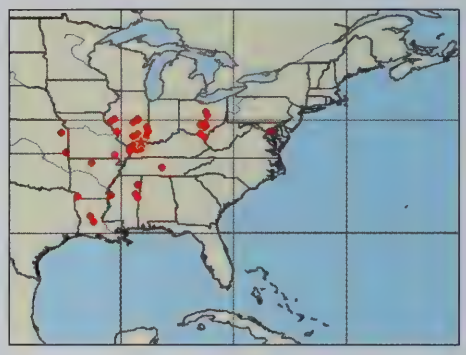
Distribution: Central and eastern USA.

Host plants: *Vitis* spp.

Note: The species name "*ortha,*" meaning "straight," refers to the straight and parallel ventral processes of the aedeagus.

Figure 10. *E. ortha* sp.n.

11. ***Erythroneura festiva*** Beamer, 1938 (Fig. 11)
Erythroneura festiva Beamer, 1938:290



Description: Length 2.6–2.7 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches of subequal size. Second point of style apex well developed; third point elongate, longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, broad in lateral view, round in crossection, with dorsal carina; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes subapical, triangular. Dorsum yellow or white with orange color pattern; vertex with orange parallel submedial lines with lateral branch, midline pale; anteclypeus brown; pronotum with Y- or V-shaped medial vitta; mesonotum pale, with red lateral triangles; thoracic venter entirely dark; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype ♂, USA, Illinois, White Co., 31 III 1929 (Beamer), (KSEM).
Distribution: Central and eastern USA.
Host plants: *Vitis* spp.

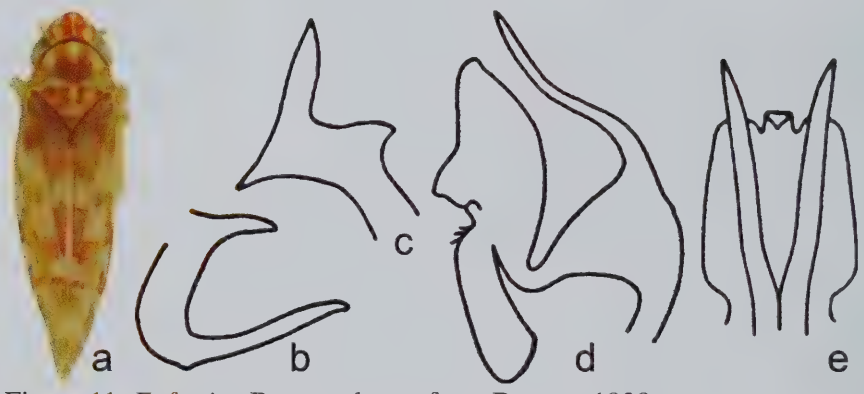
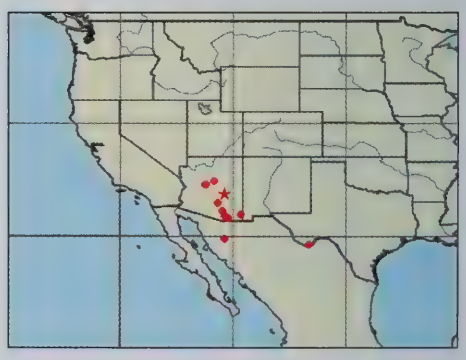


Figure 11. *E. festiva* Beamer. b–e – from Beamer 1938.

12. ***Erythroneura gilensis*** Beamer, 1929 (Fig. 12)
Erythroneura gilensis Beamer, 1929:123



Description: Length 3.2–3.4 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; pygofer dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex very short, tooth like; third point elongate, longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, broad in lateral view, round in crossection, with dorsal carina; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at apex; distal processes subapical, triangular. Coloration similar to that of *E. comes* Say.
Type locality: Holotype ♂, USA, Arizona, Gila Co., 5 VIII 1927 (Beamer), (KSEM).
Distribution: Southwestern USA, northern Mexico.
Host plants: *Vitis arizonica*.

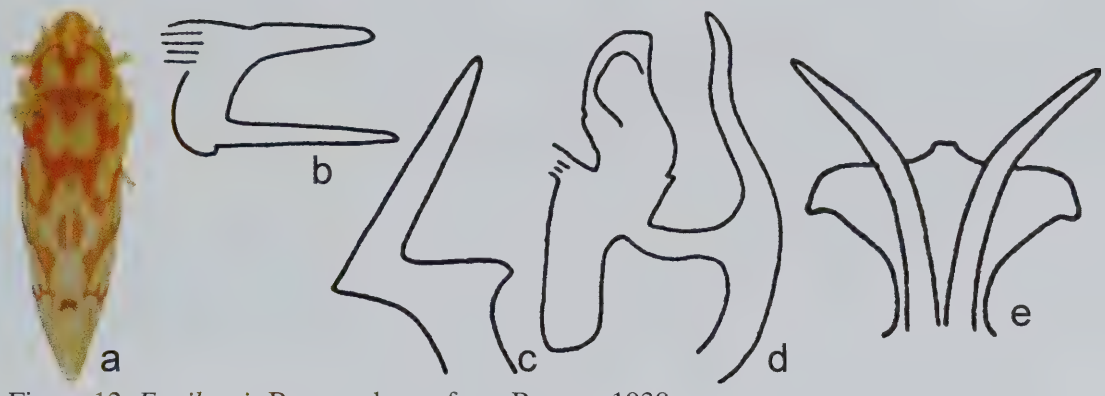
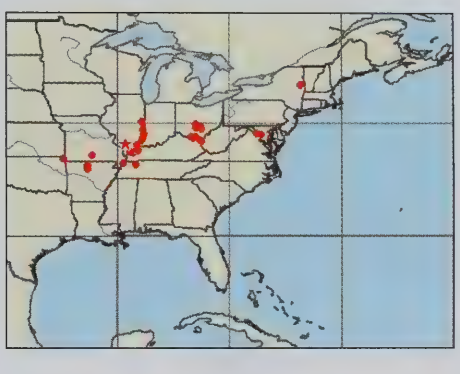


Figure 12. *E. gilensis* Beamer. b–e – from Beamer 1938.

13. ***Erythroneura pontifex*** McAtee, 1926 (Fig. 13)
Erythroneura comes var. *pontifex* McAtee, 1926:136
Erythroneura breakeyi Johnson, 1934:261
Erythroneura pontifex Beamer, 1938:279



Description: Length 2.8–3.1 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; pygofer dorsal appendages not extended beyond pygofer apex, C-shaped, with branches subequal in length. Second point of style apex very short, tooth like; third point elongate, longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, broad in lateral view, round in crossection; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at apex; distal processes subapical, triangular. Dorsum yellow or white, with reddish or brownish color pattern; vertex with large black area, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y- or V-shaped medial vitta; mesonotum pale, with red lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewing with oblique vittae forming continuous zigzag pattern; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell without brown spot.
Type locality: Holotype ♀, USA, Illinois, Washington Co., Du Bois, 24 V 1917 (McAtee), (INHS).
Distribution: Central and northeastern USA.
Host plants: *Vitis* spp.

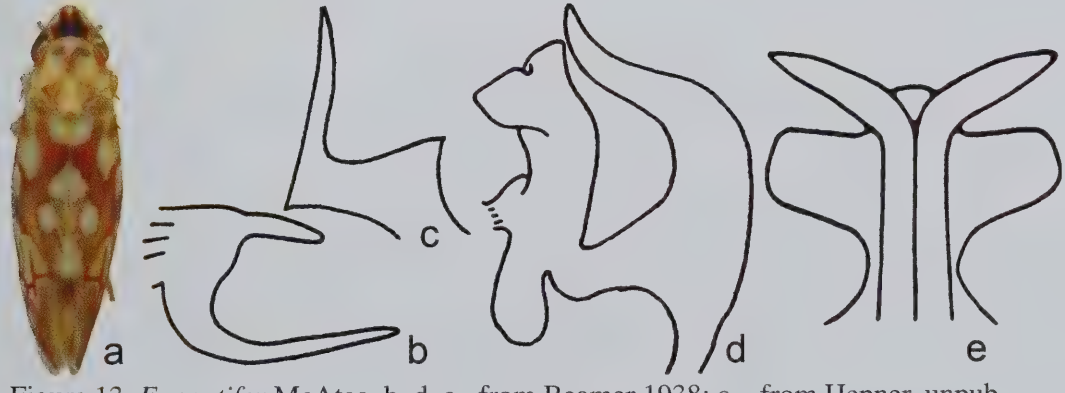
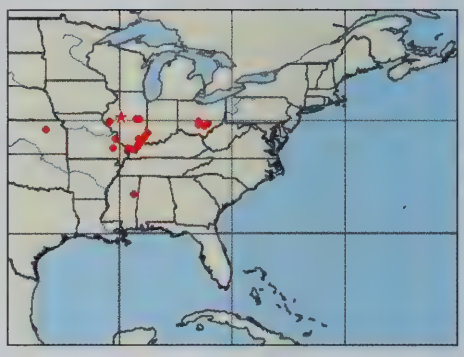


Figure 13. *E. pontifex* McAtee. b, d, e –from Beamer 1938; c – from Hepner, unpublished.

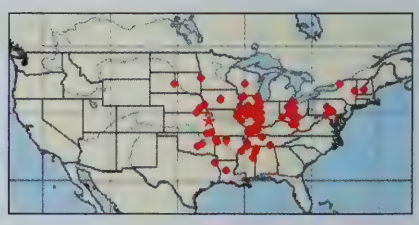
14. ***Erythroneura palimpsesta*** McAtee, 1924 (Fig. 14, Plate 1a)
Erythroneura comes var. *palimpsesta* McAtee, 1924c:43
Erythroneura palimpsesta Johnson, 1935:107



Description: Length 2.8–3 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, with branches subequal in length. Second point of style apex very short, tooth like; third point elongate, longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, broad in lateral view, round in crossection, with dorsal carina not reaching aedeagus apex; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at apex; distal processes apical, triangular. Dorsum yellow or white with reddish brown color pattern; vertex with parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y- shaped medial vitta; mesonotum pale, with dark lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewing with oblique vittae forming continuous zigzag pattern; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype ♂, USA, Illinois, Mason Co., Forest City, 3 IV 1917 (McAtee), (INHS).
Distribution: Central and eastern USA.
Host plants: *Parthenocissus quinquefolia*.

Figure 14. *E. palimpsesta* McAtee. b–e – from Beamer 1938.

15. ***Erythroneura beameri*** Robinson, 1924 (Fig. 15)
Erythroneura beameri Robinson, 1924a:61



Description: Length 2.8–3.2 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, with branches subequal in length. Second point of style apex very short, tooth like; third point elongate, longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, broad in lateral view, round in crossection; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at apex; distal processes apical, triangular. Dorsum yellow or white with orange or reddish color pattern; vertex with oblique lateral vittae, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum pale, with reddish lateral triangles; thoracic venter entirely pale; forewing with oblique vittae forming zigzag pattern; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype ♂, USA, Kansas, Douglas Co., XI 1923, (Beamer), (KSEM).
Distribution: Central and eastern USA, southeastern Canada.
Host plants: *Vitis* spp.

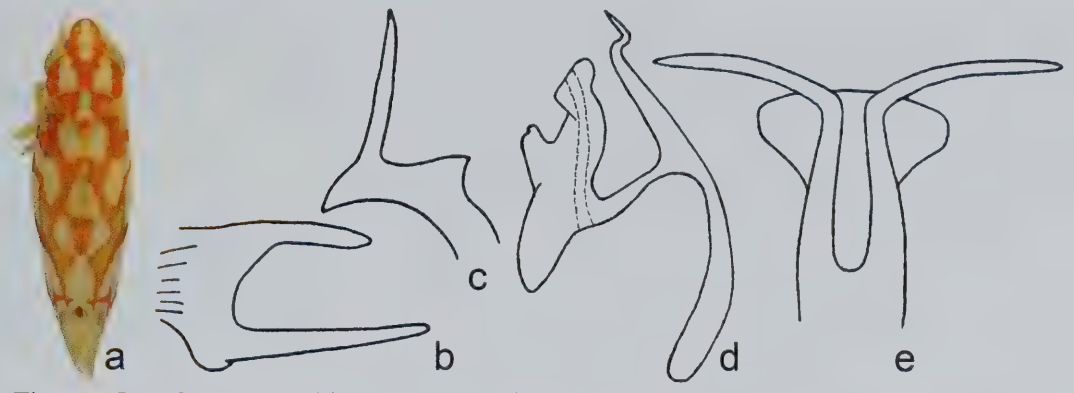
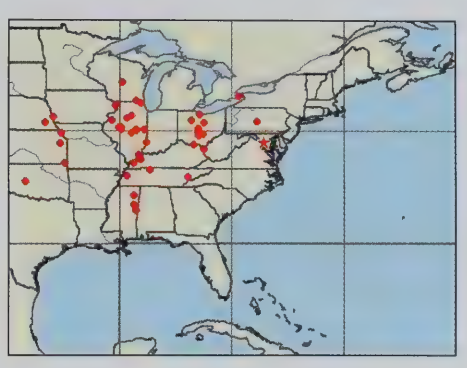


Figure 15. *E. beameri* Robinson. b, c, e – from Beamer 1938; d – Hepner, unpublished.

16. ***Erythroneura reflecta*** McAtee, 1924 (Fig. 16)
Erythroneura comes var. *reflecta* McAtee, 1924c:43
Erythroneura portea Robinson, 1924b:154
Erythroneura reflecta Beamer, 1938:283



Description: Length 3–3.3 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; pygofer dorsal appendages not extended beyond pygofer apex, C-shaped, with branches subequal in length. Second point of style apex very short, tooth like; third point of style apex elongate, longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, broad in lateral view, round in crossection, with dorsal carina, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, compressed in basal half, divergent at apex; distal processes apical, triangular. Dorsum yellow or white with reddish or brownish color pattern; vertex with orange parallel submedial lines with lateral branch, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with V-shaped medial vitta; mesonotum pale, with dark lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewing with oblique vittae forming continuous zigzag pattern; clavus largely or entirely red or brown; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype ♀, USA, Maryland, Montgomery Co., Plummers Island, 14 XII 1913 (McAtee), (USNM).
Distribution: Central and eastern USA, southeastern Canada.
Host plants: *Vitis* spp.

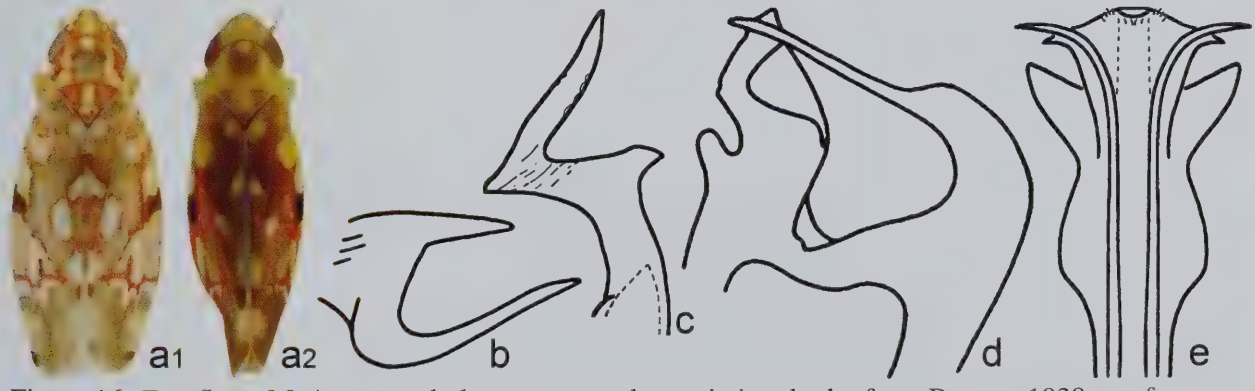
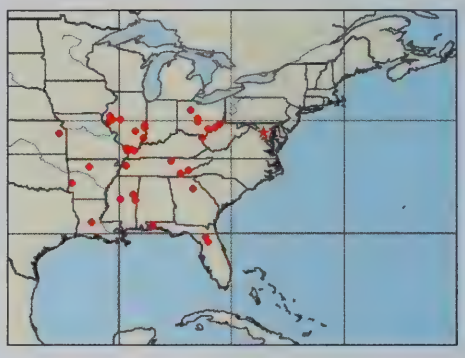


Figure 16. *E. reflecta* McAtee. a1 – holotype; a2 – color variation. b, d – from Beamer 1938; c – from Young 1952.

17. ***Erythroneura integra*** McAtee, 1920 (Fig. 17)
Erythroneura tricincta var. *integra* McAtee, 1920:309
Erythroneura integra Beamer, 1938:271



Description: Length 2.8–3.2 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, ventral branch much longer than dorsal. Second point of style apex longer than third; third point short; angle between basal and third points more than 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, broad in lateral view, round in crossection, denticulate distally; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes subapical, triangular. Dorsum yellow or white, with reddish or brown color pattern; vertex with orange parallel submedial lines (often with lateral branch), midline pale; anteclypeus pale, concolorous with rest of face; pronotum almost entirely dark; mesonotum pale, with reddish lateral triangles; thoracic venter entirely pale; forewings with oblique vitae, narrow crossband, and darkened apices; dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.
Type locality: Holotype ♀, USA, Maryland, Montgomery Co., Plummers Island, 28 III 1915 (McAtee), (USNM).
Distribution: Central and eastern USA.
Host plants: *Vitis* spp.

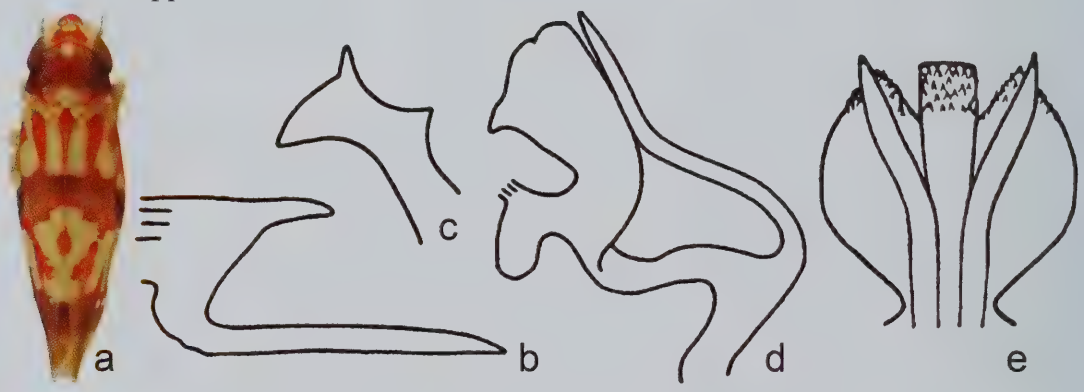
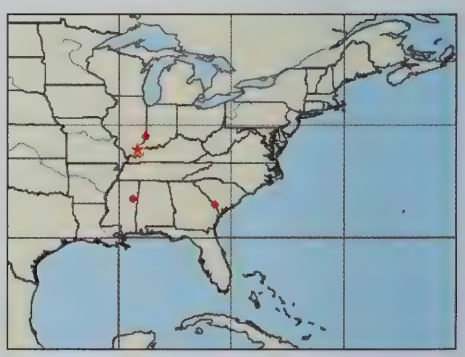


Figure 17. *E. integra* McAtee. b–e – from Beamer 1938.

18. ***Erythroneura carinata*** Dmitriev & Dietrich **sp.n.** (Fig. 18)



Description: Length 3–3.2 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex longer than third; third point short; angle between basal and third points about 90°. Dorsal apodeme broadly expanded in lateral view, triangular in ventral view, without distinct connection to anal tube or pygofer appendages. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, broad in lateral view, compressed in crossection, with strong dorsal keel, extended far beyond bases of distal processes, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes long, subapical, flattened, triangular. Dorsum yellow or white, with reddish and brown color pattern; vertex with orange parallel submedial lines (often with lateral branch), midline pale; anteclypeus pale, concolorous with rest of face; pronotum almost entirely dark; mesonotum entirely dark, scutellum pale, contrasting with rest of mesonotum; thoracic venter entirely pale; forewing with oblique vitae, narrow brown crossband, and darkened apices; dark spot at costal margin; apical cell II with distal spot; inner apical cell without brown spot.

Diagnosis: *E. carinata* n.sp. is similar to *E. diva* McAtee and *E. cymbium* McAtee, but the aedeagus has a strong dorsal keel and its apex extends far beyond the bases of the distal processes.
Type locality: Holotype ♂, USA, Illinois, White Co., Gossett, 13 IV 1960 (Ross & Cunningham), (INHS).
Studied material: Paratypes 23 ♂, 3 ♀, USA, Illinois, White Co., Gossett, 13 IV 1960 (Ross & Cunningham), (INHS); other studied material from Georgia, Illinois, and Mississippi excluded from type series.
Distribution: Central and southeastern USA.
Host plants: *Vitis* sp.
Note: The species name "*carinata,*" meaning "keeled," refers to the dorsally keeled aedeagal shaft.

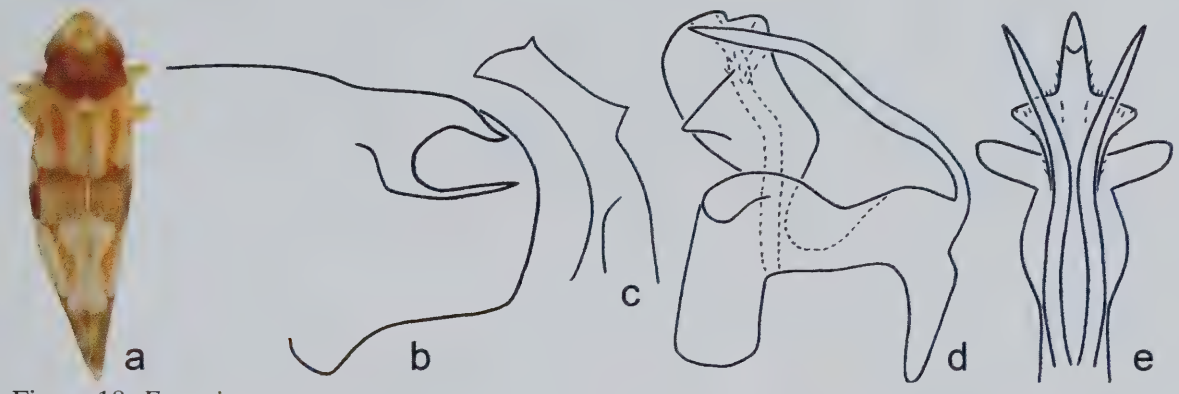
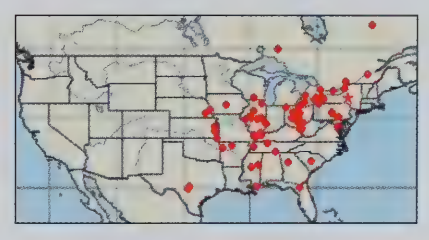


Figure 18. *E. carinata* sp.n.

19. ***Erythroneura tricincta*** Fitch, 1851 (Fig. 19)
Erythroneura tricincta Fitch, 1851:63
Erythroneura tricincta var. *a* Fitch, 1851:63
Threebanded leafhopper



Description: Length 2.9–3.3 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex longer than third; third point shorter than second; angle between basal and third points about 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, broad in lateral view, round in crossection; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes subapical, triangular. Dorsum yellow or white, with reddish and brown color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum mostly dark. Mesonotum dark basally, scutellum pale; thoracic venter entirely pale; forewing with or without oblique vittae, narrow crossband and darkened apices; dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.
Type locality: Neotype ♂, USA, Kansas, Cherokee Co., 10 IV 1936 (Beamer), (KSEM), here designated
Distribution: Central and eastern USA, southeastern Canada.
Host plants: *Vitis* spp.
Note: Because Fitch's holotype is lost, we designate a neotype to stabilize the concept of this species, the type of the genus. This concept equals that of the previous revisions (Beamer 1938, Young 1952).

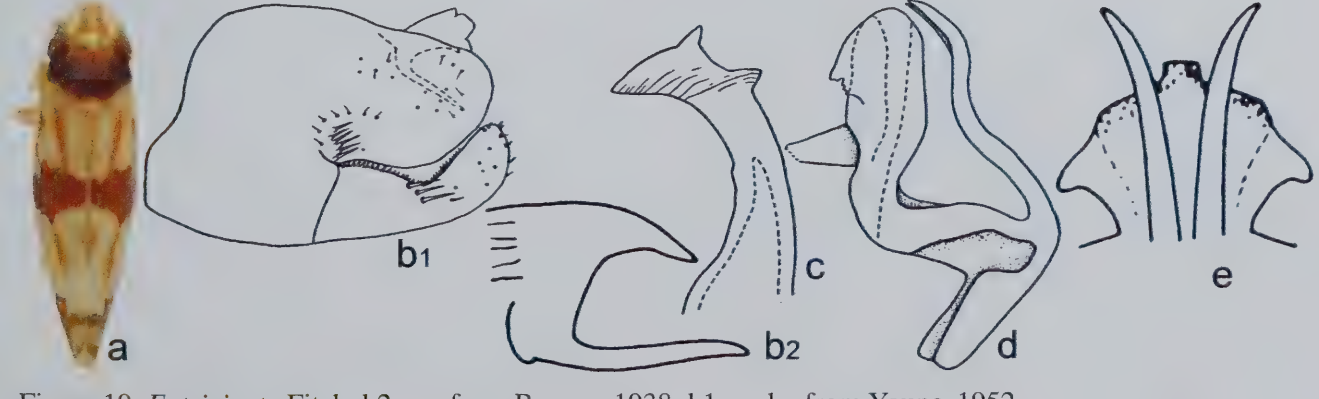
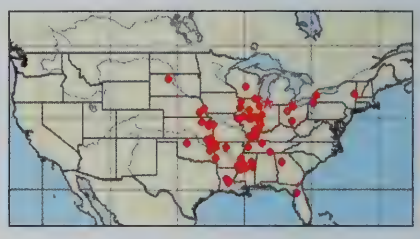


Figure 19. *E. tricincta* Fitch. b2, e – from Beamer 1938; b1, c, d – from Young 1952.

20. ***Erythroneura cymbium*** McAtee, 1920 (Fig. 20)
Erythroneura tricincta var. *cymbium* McAtee, 1920:310
Erythroneura tricincta var. *disjuncta* McAtee, 1920:310, **syn.n.**
Erythroneura cymbium Beamer, 1938:271



Description: Length 2.6–3 mm. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex longer than third; third point short; angle between basal and third points about 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, broad in lateral view, round in crossection; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes subapical, triangular. Dorsum yellow or white, with reddish and brown color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with dark posterior half, or at least posterior corners; mesonotum entirely pale; thoracic venter entirely pale; forewings with or without oblique vittae, with narrow crossband, and darkened apices; dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.
Type locality: Holotype ♀, USA, Michigan, Berrien Co., Benton Harbor, on *Vitis* sp., 28 V 1912 (Seigler), (USNM).
Distribution: Central and eastern USA, southeastern Canada.
Host plants: *Vitis* spp.

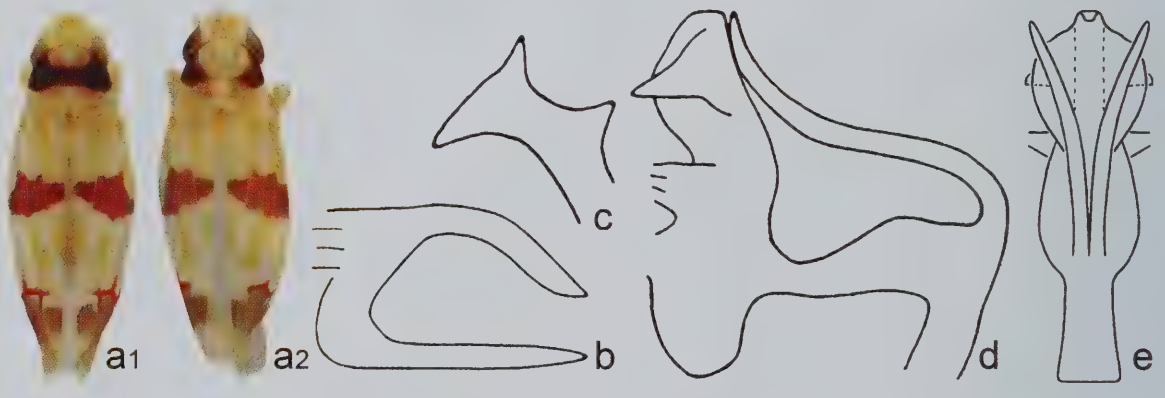
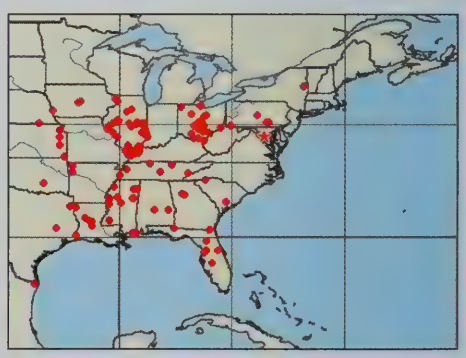


Figure 20. *E. cymbium* McAtee. a2 – var. *disjuncta*. b–d – from Beamer 1938.

21. ***Erythroneura calycula*** McAtee, 1920 (Fig. 21, Plate1b)
Erythroneura tricincta var. *calycula* McAtee, 1920:308
Erythroneura tricincta var. *erasa* McAtee, 1920:309, **syn.n.**
Erythroneura calycola Osborn, 1932:515, missp.
Erythroneura tricincta var. *noncincta* Johnson, 1934:261, **syn.n.**
Erythroneura calycula Beamer, 1938:270



Description: Length 2.6–3 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex longer than third; third point short; angle between basal and third points about 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, slender in lateral view; depressed in crossection; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes apical, triangular. Dorsum yellow or white, with reddish and brown color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with dark posterior corners; mesonotum with dark lateral triangles, or base entirely dark, scutellum pale; thoracic venter entirely pale; forewings with or without oblique vittae, with narrow crossband, and darkened apices; dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.

Type locality: Holotype ♂, USA, Maryland, Montgomery Co., Plummers Island, 14 XII 1913 (McAtee), (USNM).
Distribution: Central and eastern USA.
Host plants: *Vitis* spp.

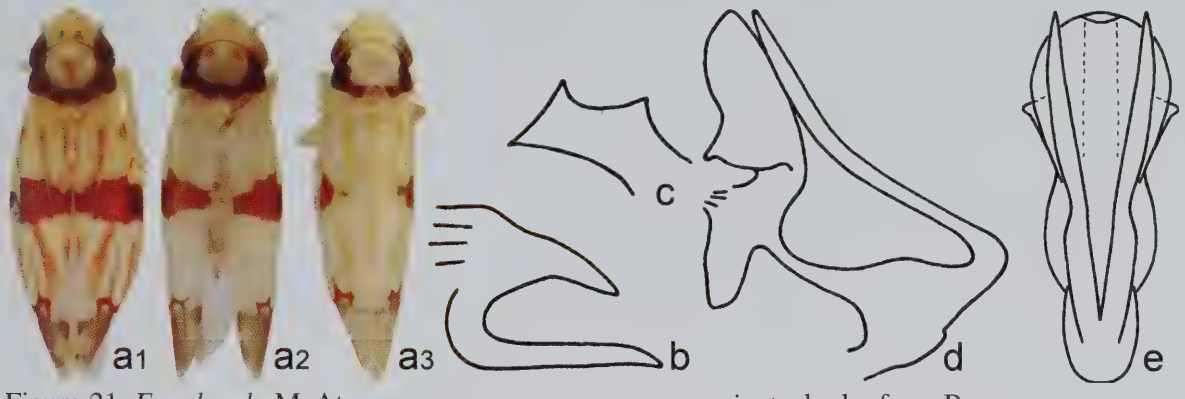
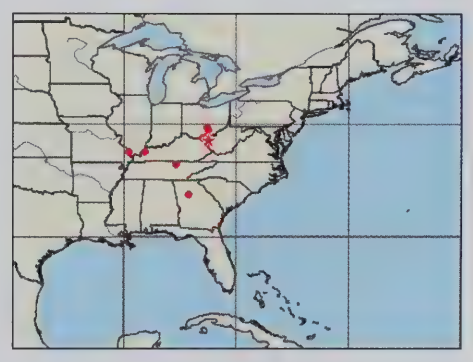


Figure 21. *E. calycula* McAtee. a2 – var. *erasa*; a3 – var. *noncincta*. b, d – from Beamer 1938; c – from Hepner, unpublished.

22. ***Erythroneura vagabunda*** Knull, 1945 (Fig. 22)
Erythroneura vagabunda Knull, 1945:109



Description: Length 2.9–3.1 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point elongate, longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, slender in lateral view, denticulate distally, round in crossection; ventral processes placed basally, well separated from shaft, longer than shaft, evenly divergent; distal processes long, subapical, slender. Dorsum yellow or white with orange color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum pale, with orange lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewing with broken oblique vittae; clavus with separate basal and distal vittae and dark brown spot near midlength; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype ♂, USA, Ohio, Lawrence Co., 29 IV 1934 (Caldwell), (OSU).
Distribution: Central and eastern USA.
Host plants: Unknown.

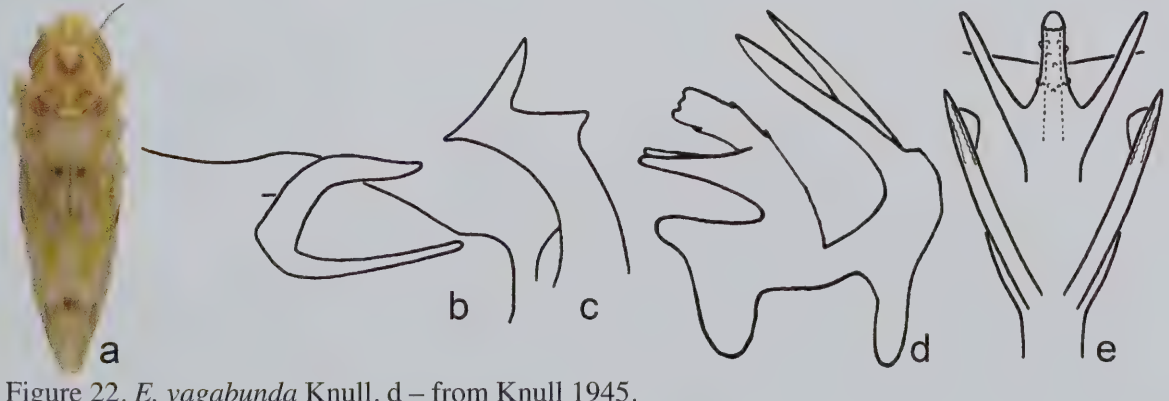
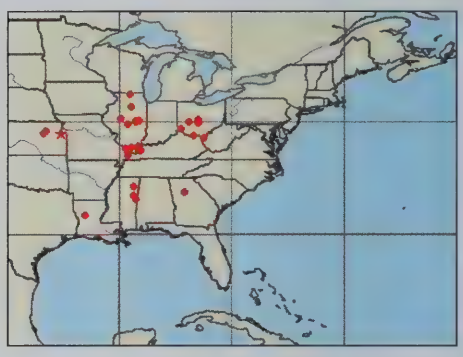


Figure 22. *E. vagabunda* Knull. d – from Knull 1945.

23. ***Erythroneura aza*** Robinson, 1924 (Fig. 23)
Erythroneura aza Robinson, 1924c:291



Description: Length 2.9–3.1 mm. Abdomen. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point elongate, longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft straight and slender in lateral view, round in crossection; apex slightly broadened in ventral view; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes long, subapical, slender. Dorsum yellow or white, with orange or reddish color pattern; vertex with parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum pale, with orange lateral triangles; thoracic venter entirely pale or with dark mesosternum; forewing with oblique vittae forming zigzag pattern; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype ♂, USA, Kansas, Douglas Co., Lawrence, 15 XII 1923 (Robinson), (KSEM).
Distribution: Central and eastern USA.
Host plants: *Vitis* spp.

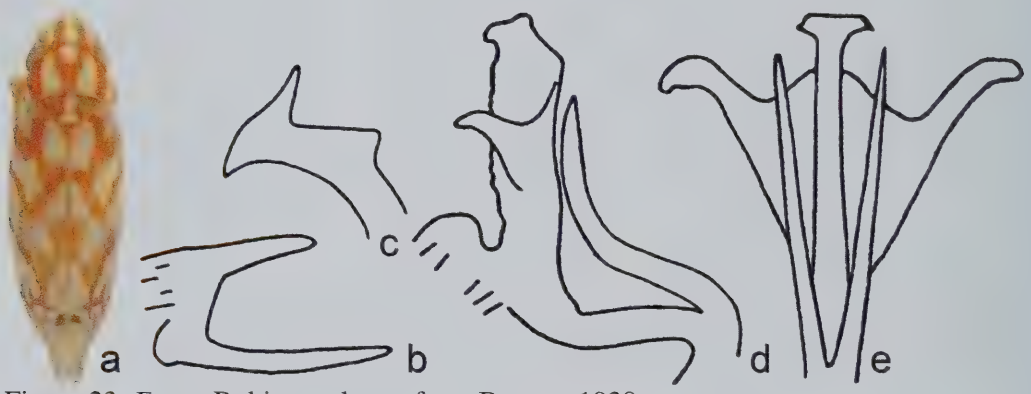
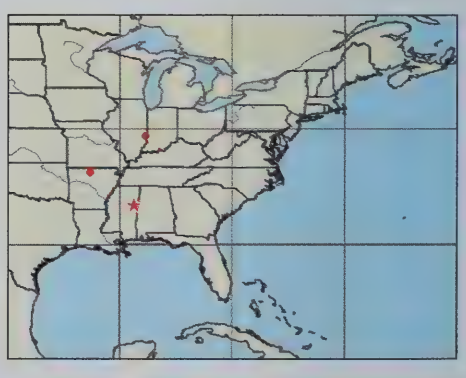


Figure 23. *E. aza* Robinson. b–e – from Beamer 1938.

24. ***Erythroneura glabra*** Dmitriev & Dietrich **sp.n.** (Fig. 24)



Description: Length 2.8–3 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft symmetrical, curved dorsally, broad in lateral view, round in crossection; apex truncate in posterior view; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes long, subapical, slender. Coloration similar to that of *E. comes* Say: dorsum yellow or white with orange color pattern; vertex with orange parallel submedial lines (often with lateral branch), midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y- or V-shaped medial vitta; mesonotum pale, with orange lateral triangles; thoracic venter entirely pale; forewings with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Diagnosis: The coloration of new species similar to that of *E. comes* Say, and the male genitalia resemble those of *E. vagabunda* Knull, but the aedeagus shaft lacks distal denticuli and the ventral processes are parallel to each other.

Type locality: Holotype ♂, USA, Mississippi, Oktibbeha Co., State College, 4 I 1962 (Hepner), (INHS).
Studied material: Paratypes, 1 ♂, USA, Arkansas, Marion Co., Yellville, on *Cornus sp.*, 23 VIII 1962 (Hepner), (MEM); 1 ♂, Illinois, Clark Co., Rocky Branch, 25 VII 1954 (Cunningham), (INHS).
Distribution: Central and southeastern USA.
Host plants: Unknown.
Note: The species name "*glabra,*" meaning "bare," refers to the lack of denticuli on the apex of the aedeagal shaft.

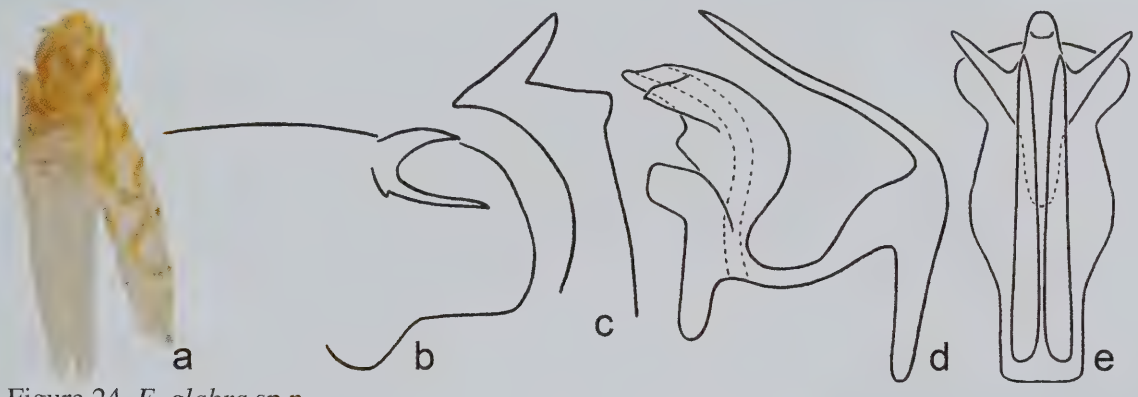
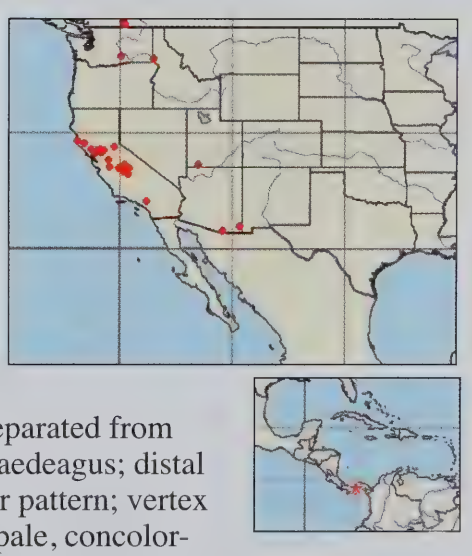


Figure 24. *E. glabra* sp.n.

25. ***Erythroneura elegantula*** Osborn, 1928 (Fig. 25)
Erythroneura elegantula Osborn, 1928a:289
Western grape leafhopper



Description: Length 2.8–3 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex longer than third; third point elongate, longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, broad in lateral view, compressed in crossection, with dorsal carina; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes, triangular. Dorsum yellow or white, with orange color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum pale, with black lateral triangles; thoracic venter entirely pale or with dark mesosternum; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype ♀, Panama, Canal Zone (CMNH). Type was not studied.
Distribution: Western USA, southwestern Canada, Panama (apparently introduced).
Host plants: *Vitis* spp.

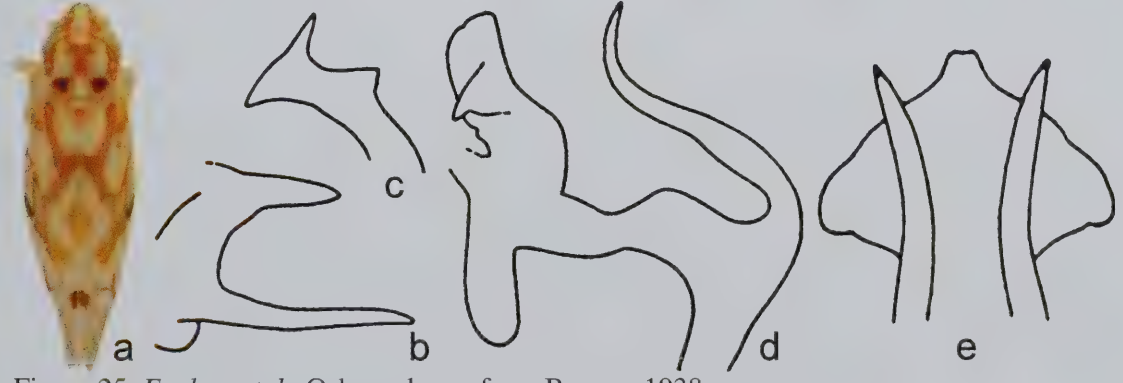
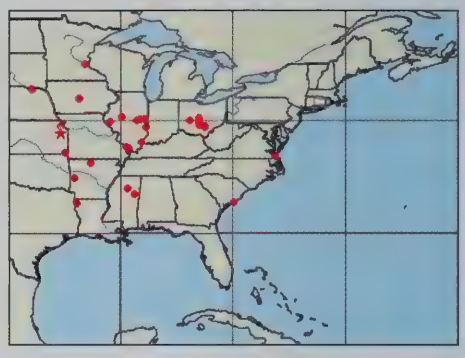


Figure 25. *E. elegantula* Osborn. b–e – from Beamer 1938.

26. ***Erythroneura acuticephala*** Robinson, 1924 (Fig. 26, Plate 1c)
Erythroneura acuticephala Robinson, 1924a:61



Description: Length 2.6–2.9 mm. Abomen. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point elongate, longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, broad in lateral view; compressed in crossection; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes apical, triangular. Dorsum yellow or white, with reddish or orange color pattern; vertex with parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum pale, with orange lateral triangles; thoracic venter entirely pale; forewing with oblique vittae forming continuous zigzag pattern; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype ♂, USA, Kansas, Douglas Co., XII 1923, (Robinson), (KSEM).
Distribution: Central and eastern USA.
Host plants: *Vitis* spp.

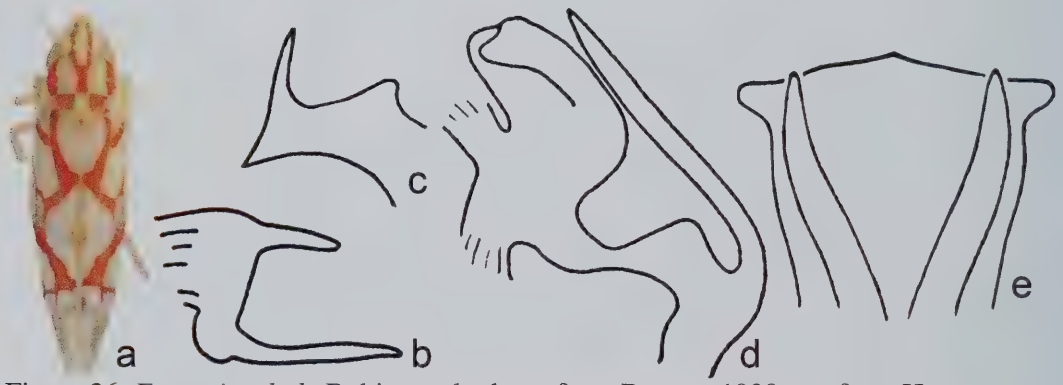
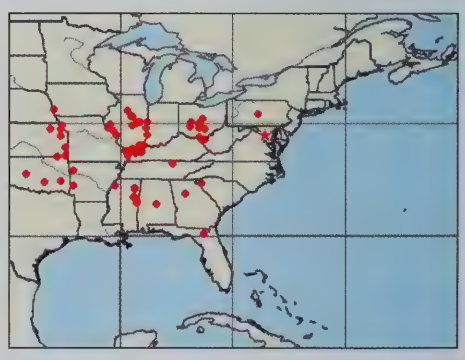


Figure 26. *E. acuticephala* Robinson. b, d, e – from Beamer 1938; c – from Hepner, unpublished.

27. **Erythroneura aclys** McAtee, 1920 (Fig. 27)
Erythroneura aclys McAtee, 1920:290



Description: Length 2.7–3.1 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, broad in lateral view, round in crossection; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at apex; distal processes subapical, triangular. Dorsum yellow or white, with brown color pattern; vertex with large basal dark area, often extended onto thorax, midline dark; anteclypeus pale, concolorous with rest of face; pronotum dark with pale lateral margins; mesonotum entirely dark; thoracic venter entirely pale; forewings with oblique vittae forming continuous zigzag pattern; clavus largely brown; dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.
Type locality: Holotype ♂, USA, Maryland, Montgomery Co., Plummers Island, 21 XII 1913 (McAtee), (USNM). Type was not studied.
Distribution: Central and eastern USA.
Host plants: *Cercis canadensis*.

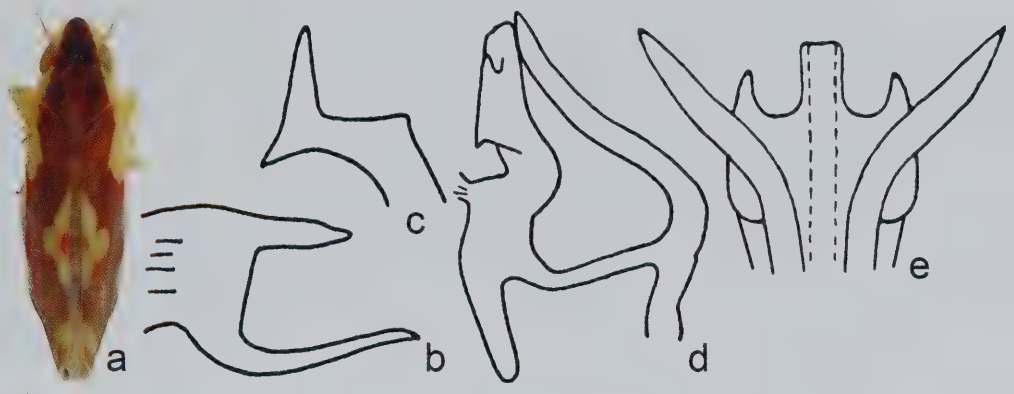
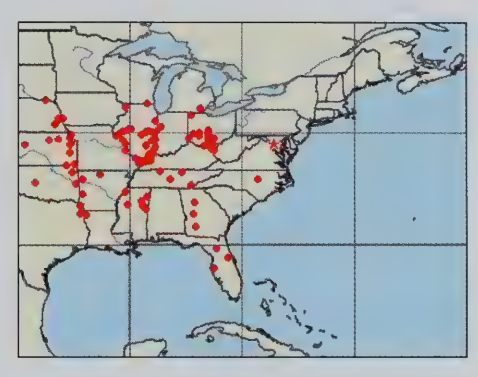


Figure 27. *E. aclys* McAtee. b–e – from Beamer 1938; a – original.

28. ***Erythroneura bistrata*** McAtee, 1920 (Fig. 28)
Erythroneura vitis var. *bistrata* McAtee, 1920:305
Erythroneura vitis var. *stricta* McAtee, 1920:306
Erythroneura rubranotum Robinson, 1924a:60
Erythroneura bistrata Johnson, 1934:262
Erythroneura vitis var. *fusco-clava* Beamer, 1927:31



Description: Body. Size 2.9–3.2 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point elongate, longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, slender in lateral view, round in crossection, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at apex; distal processes subapical, triangular. Dorsum yellow or white with reddish brownish color pattern, which strongly vary; vertex unicolorous pale or darkened posteriorly, midline pale; anteclypeus pale, concolorous with rest of face; pronotum almost entirely dark; mesonotum dark, with pale scutellum; thoracic venter entirely pale; forewing mostly dark with small pale spots or with two narrow pale crossbands; dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.
Type locality: Holotype ♂, Maryland, Montgomery Co., Plummers Island, 28 III 1915 (McAtee), (USNM).
Distribution: Central and eastern USA.
Host plants: *Cercis canadensis*.

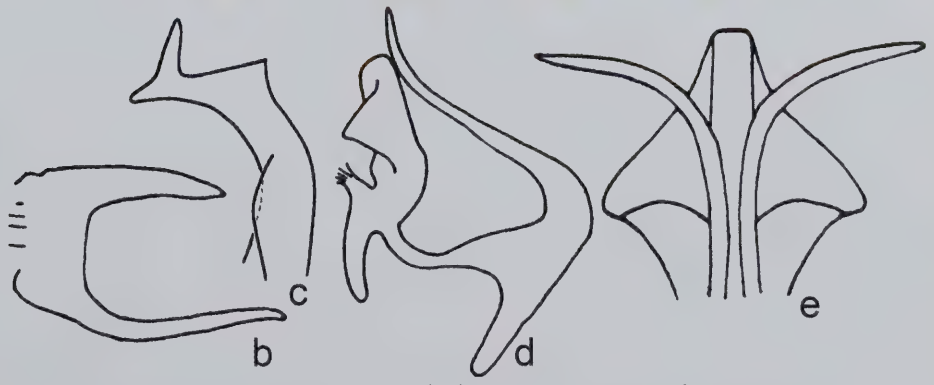
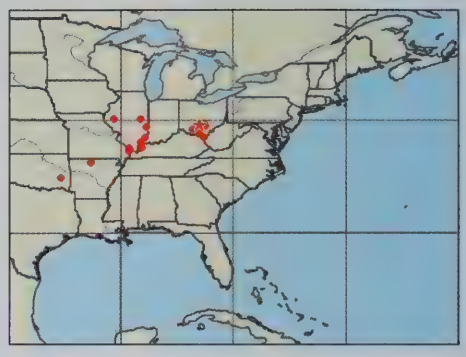


Figure 28. *E. bistrata McAtee*. a1 – holotype, a2 – var. *stricta*, a3 – var. *rubranota*, a4 – color variation. b, d, e – from Beamer 1938.

29. ***Erythroneura prosata*** Johnson, 1935 (Fig. 29)
Erythroneura infuscata var. *prosata* Johnson, 1935:108
Erythroneura prosata DeLong & Caldwell, 1937:81



Description: Length 2.8–3 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point elongate, longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, slender in lateral view, round in crossection, with dorsal carina, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at apex; distal processes subapical, triangular. Dorsum yellow or white, with reddish brown color pattern; vertex mostly dark, midline dark; anteclypeus pale, concolorous with rest of face; pronotum almost entirely dark; mesonotum with dark lateral triangles and dark apex of scutellum; thoracic venter with dark mesosternum, remainder pale; forewings mostly dark with small pale spots; dark spot at costal margin; apical cell II with distal spot; inner apical cell without brown spot.
Type locality: Holotype ♂, USA, Ohio, Pickaway Co., 31 III 1934 (Caldwell), (OSU).
Distribution: Central USA.
Host plants: *Rubus* spp. (?).

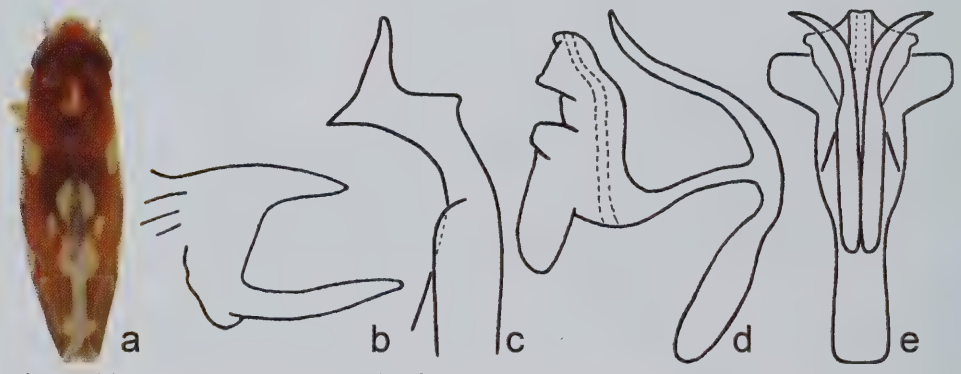
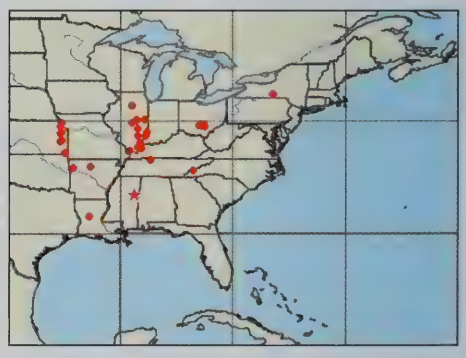


Figure 29. *E. prosata* Johnson. b –from Beamer 1938; d – from Hepner, unpublished.

30. ***Erythroneura infuscata*** (Gillette, 1898) (Fig. 30, Plate 1d)
Typhlocyba comes var. *infuscata* Gillette, 1898:764
Erythroneura comes var. *infuscata* Van Duzee, 1916:77
Erythroneura infuscata McAtee, 1920:302



Description: Length 2.8–3 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point elongate, not longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, broad in lateral view, compressed in crossection, with strong dorsal keel; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at apex; distal processes subapical, triangular. Dorsum mostly black, with small pale spots at middle of mesonotum and at costal margin of wings; anteclypeus pale, concolorous with rest of face; thoracic venter entirely dark.
Type locality: Holotype ♀, USA, Mississippi, Oktibbeha Co., Agriculture College (MSU), (USNM).
Distribution: Central and eastern USA.
Host plants: Unknown.

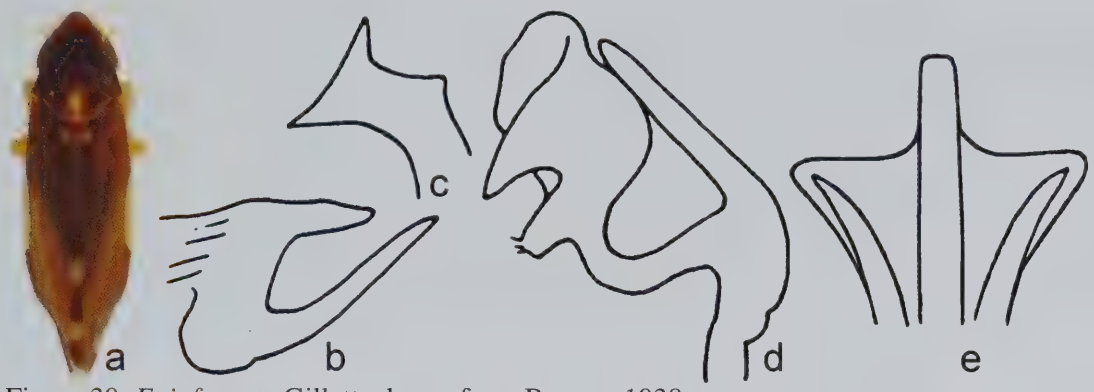
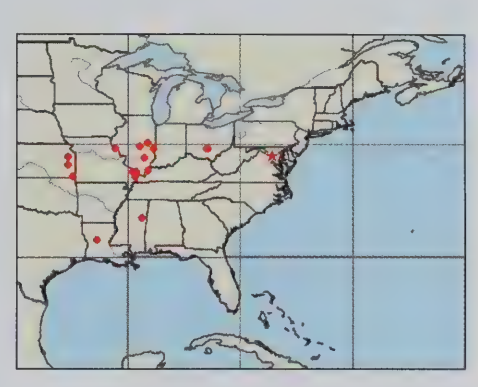


Figure 30. *E. infuscata* Gillette. b–e – from Beamer 1938.

31. ***Erythroneura cancellata*** McAtee, 1920 (Fig. 31)
Erythroneura comes var. *cancellata* McAtee, 1920:320
Erythroneura cancellata Robinson, 1926:141



Description: Length 3.2–3.4 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, ventral branch about twice as long as dorsal branch. Second point of style apex well developed; third point subequal in size with second; angle between basal and third points about 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, slender in lateral view, round in crossection, with dorsal carina; ventral processes placed basally, well separated from shaft, longer than shaft, divergent only at apex; distal processes subapical, triangular. Dorsum yellow or white, with orange and brown color pattern; vertex with large basal dark area, often extended onto thorax, midline dark; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta or almost entirely dark; mesonotum pale, with brown lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewings with pale diamond-shaped transcommisural marking outlined with dark brown, with oblique vittae forming zigzag pattern; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.

Type locality: Holotype ♀, USA, Maryland, Montgomery Co., Plummers Island, 30 XI 1913 (McAtee), (USNM).

Distribution: Central and eastern USA.

Host plants: *Cercis canadensis.*

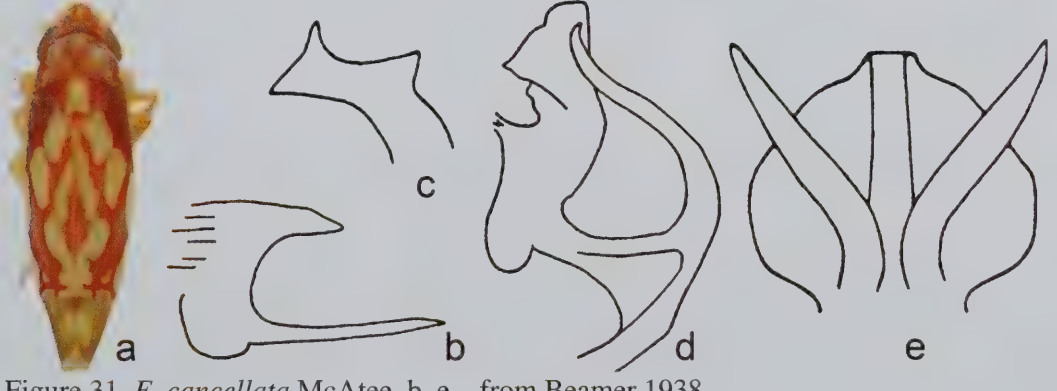


Figure 31. *E. cancellata* McAtee. b–e – from Beamer 1938.

32. ***Erythroneura triapitsyni*** Dmitriev & Dietrich **sp.n.** (Fig. 32)
Description: Length 2.7–2.9 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex longer than third; third point elongate, not longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft symmetrical, curved dorsally, broad in lateral view, smooth, round in crossection, with dorsal carina; apex truncate in posterior view; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at apex; distal processes long, subapical, flattened, triangular. Coloration similar to that of *E. elegantula* Osborn: dorsum yellow or white, with orange color pattern; vertex with orange parallel submedial lines (often with lateral branch), midline pale; anteclypeus pale, concolorous with rest of face; pronotum with V-shaped medial vitta; mesonotum pale, with black lateral triangles; thoracic venter entirely pale; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Diagnosis: The coloration of *E. triapitsyni* sp.n. is similar to that of *E. elegantula* Osborn. The male genitalia are similar to those of *E. bakeri* sp.n. but the aedeagus is round in crossection.
Type locality: Holotype ♂, USA, New Mexico, Bernalillo Co., Albuquerque, Los Ranchos de Albuquerque, 4920 Rio Grande Blvd. NW, Anderson Valley, 35.084°N 106.651°W, on *Vitis sp. (cultivated)*, 26 IX 2005 (Triapitsyn), (INHS).
Studied material: Paratypes: 7 ♂, 11 ♀, same locality as holotype, 26–28 IX 2005 (Triapitsyn), (INHS).
Distribution: New Mexico.
Host plants: *Vitis* spp.
Note: The species is named for Dr. Serguei Triapitsyn (University of California, Riverside), who collected the type series.

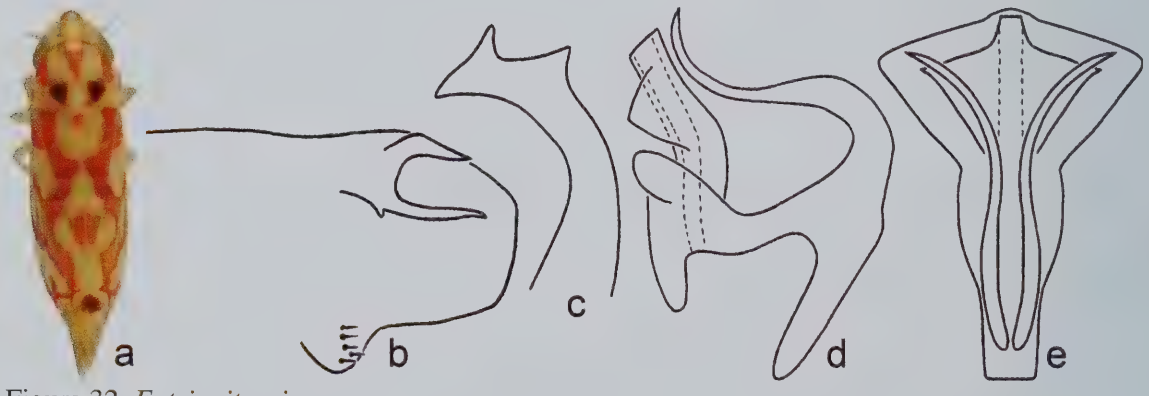
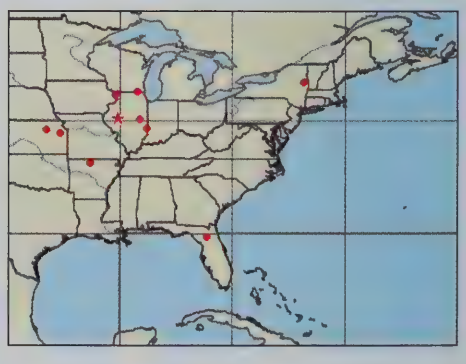


Figure 32. *E. triapitsyni* sp.n.



33. ***Erythroneura bakeri*** Dmitriev & Dietrich **sp.n.** (Fig. 33)
Description: Length 2.7–2.8 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point elongate, not longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft symmetrical, curved dorsally, broad in lateral view, smooth, compressed in crossection, with dorsal carina; apex truncate in posterior view; ventral

processes placed basally, well separated from shaft, longer than shaft, divergent at apex; distal processes long, subapical, flattened, triangular. Dorsum yellow or white, with red or orange color pattern; vertex with parallel submedial lines (often with lateral branch), midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum entirely pale; thoracic venter with dark mesosternum, remainder pale; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.

Diagnosis: *E. bakeri* sp.n. is similar to *E. triapitsyni* sp.n., but the aedeagus has a stronger dorsal carina, and the mesonotum lacks black lateral triangles.

Type locality: Holotype ♂, USA, Illinois, Fulton Co., Anderson Lake State Conservation Area, 8 IX 1954 (Ross), (INHS).

Studied material: Paratypes, 2 ♂, Illinois, Clark Co., Darwin, on *Quercus lyrata*, 15 IX 1953 (Ross), (INHS); 6 ♂, Illinois, Fulton Co., Anderson Lake State Conservation Area, 8 IX 1954 (Ross), (INHS), 2 ♂, Illinois, Jo Daviess Co., Blanding, on *Prunus virginiana*, 28 IV 1954 (Ross), (INHS); other studied material from Wisconsin, Kansas, Arkansas, Illinois, New York, and Florida excluded from type series.

Distribution: Central and eastern USA.

Host plants: *Vitis* spp.

Note: This species is named in memory of C.F. Baker (1872–1927), a pioneer in the study of Auchenorrhyncha.

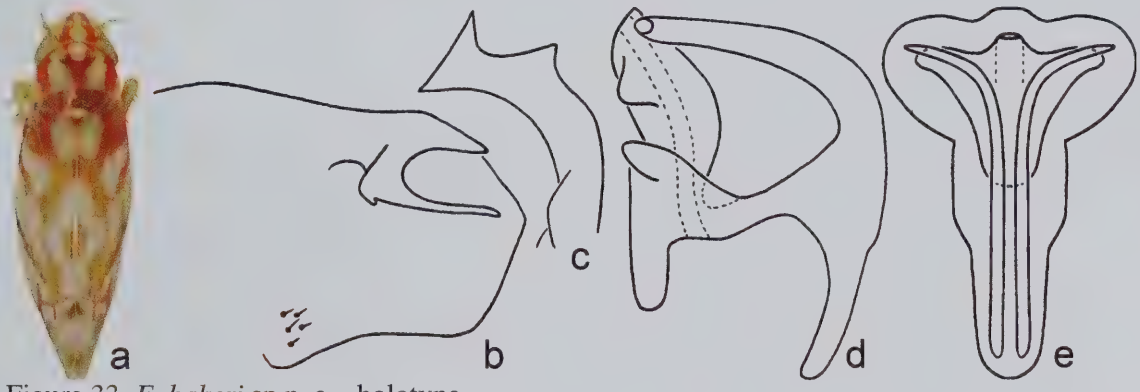
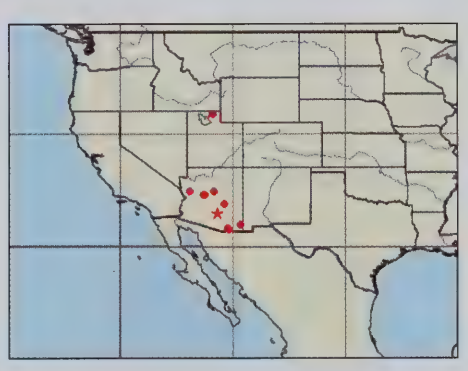


Figure 33. *E. bakeri* sp.n. a – holotype.

34. ***Erythroneura anfracta*** Beamer, 1929 (Fig. 34)

Erythroneura anfracta Beamer, 1929:123



Description: Length 3.1–3.3 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe angulate; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex longer than third; third point short; angle between basal and third points about 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, broad in lateral view; compressed in crossection, with strong dorsal keel; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side; distal processes subapical, triangular. Dorsum yellow or white, with orange, reddish, or brownish color pattern; vertex with parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum pale, with dark lateral triangles; scutellum pale; thoracic venter with dark mesosternum, remainder pale; forewings with oblique vittae forming continuous zigzag pattern or interrupted with pale crossband; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.

Type locality: Holotype ♂, USA, Arizona, Pinal Co., 6 VIII 1927 (Beamer), (KSEM).
Distribution: Arizona, Utah.
Host plants: *Vitis arizonica*.

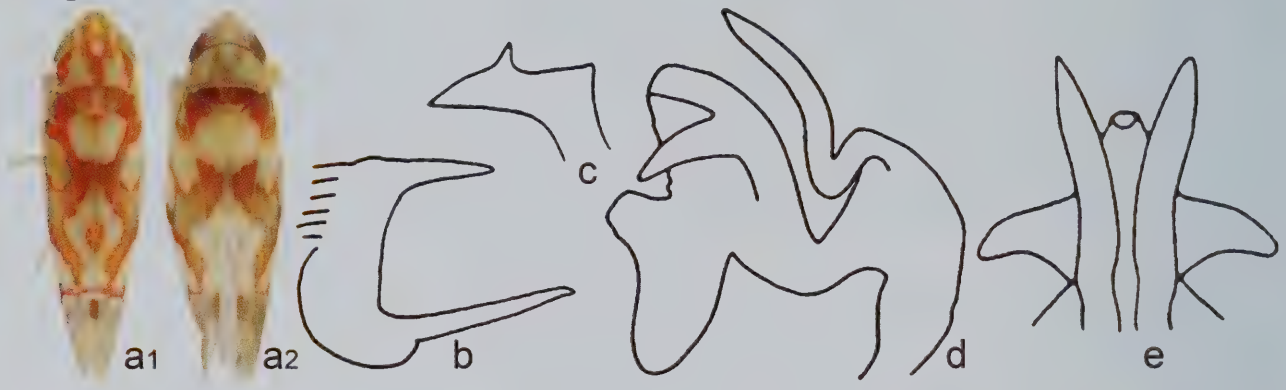
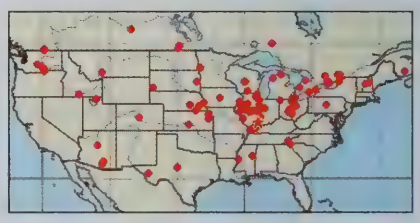


Figure 34. *E. anfracta* Beamer. a2 – color variation. b–e – from Beamer 1938.

35. **Erythroneura ziczac** Walsh, 1862 (Fig. 35)
Erythroneura ziczac Walsh, 1862:149
Typhlocyba zigzag Wirtner, 1904:227, missp.
Erythroneura ziczac Beamer, 1938:276, neotype designation
Erythroneura ziczac var. *walshi* Beamer, 1938:276, **syn.n.**
Erythroneura zizac Kaloostian, 1952:20, missp.
Virginiacreeper leafhopper



Description: Length 2.8–3.1 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe angulate; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point elongate, not longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, broad in lateral view, compressed in crossection, with strong dorsal keel, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes subapical, triangular. Dorsum yellow or white with reddish brown color pattern; vertex with parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y- or V-shaped medial vitta or almost entirely dark; mesonotum pale, with dark lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewings with oblique vittae forming continuous zigzag pattern; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Neotype ♂, USA, Illinois, Wabash Co., 31 III 1929 (Beamer), (KSEM).
Distribution: USA, southern Canada.
Host plants: *Vitis* spp.

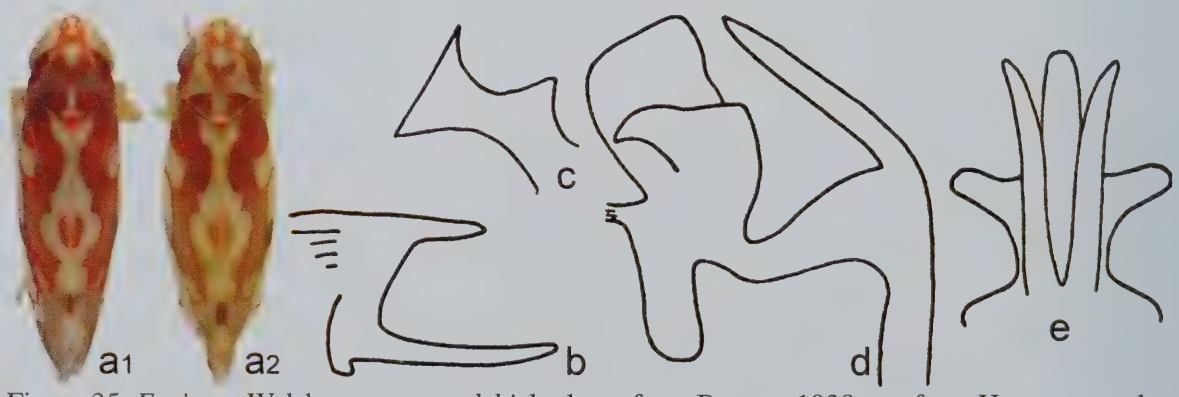
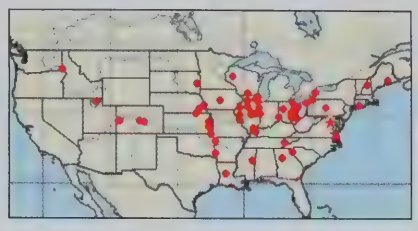


Figure 35. *E. ziczac* Walsh. a2 – var. *walshi*. b, d, e – from Beamer 1938; c – from Hepner, unpublished.

36. ***Erythroneura elegans*** McAtee, 1920 (Fig. 36)



Erythroneura comes var. *elegans* McAtee, 1920:315
Erythroneura elegans Robinson, 1926:137

Description: Length 2.7–2.9 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe angulate; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex longer than third; third point short; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, broad in lateral view, compressed in crossection, with strong dorsal keel, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes subapical, triangular. Dorsum yellow or white, with reddish brown color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum pale, with dark lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewings with oblique vittae forming zigzag pattern, pale narrow crossband at middle interrupted with red longitudinal veins; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.

Type locality: Holotype ♂, USA, Maryland, Montgomery Co., Plummers Island, 11 I 1914 (McAtee), (USNM).

Distribution: USA, southern Canada.

Host plants: *Vitis* spp.

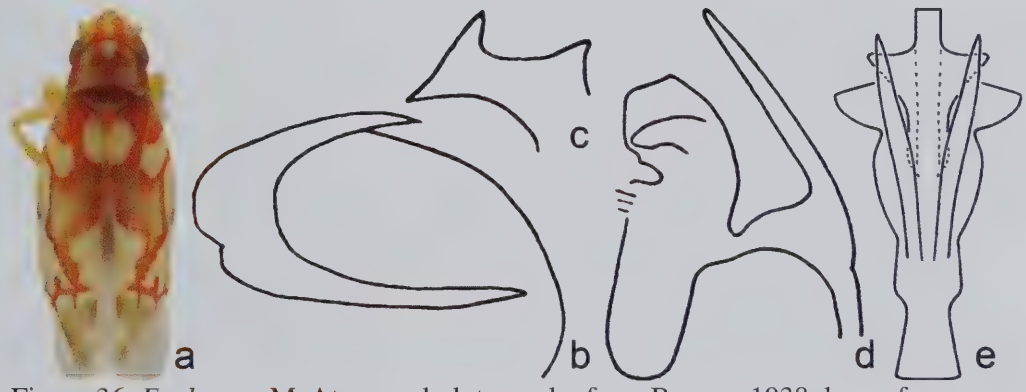
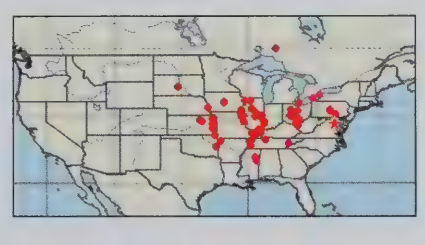


Figure 36. *E. elegans* McAtee. a – holotype. d – from Beamer 1938; b, c – from Hepner, unpublished.

37. ***Erythroneura delicata*** McAtee, 1920 (Fig. 37)



Erythroneura comes var. *delicata* McAtee, 1920:317
Erythroneura comes var. *accepta* McAtee, 1920:317, **syn.n.**
Erythroneura lacta Robinson, 1924a:62
Erythroneura scripta Robinson, 1924c:290, **syn.n.**
Erythroneura tudella Robinson, 1924c:291, **syn.n.**
Erythroneura delicata Johnson, 1935:110
Erythroneura delictata Young, 1952:80, missp.

Description: Length 2.9–3.2 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point subequal in size with second; angle between basal and third points about 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, slender in lateral view, round in crossection; apex usually broadened in ventral view; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes subapical, slender. Dorsum yellow or white, with orange color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum pale, with orange lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewing with broken oblique vittae; clavus with separate basal and distal vittae, in some cases with

dark brown spot at middle; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype ♀, USA, Maryland, Montgomery Co., Plummers Island, 26 VII 1914 (McAtee), (USNM).
Distribution: Central and northeastern USA, southeastern Canada.
Host plants: *Vitis* spp.

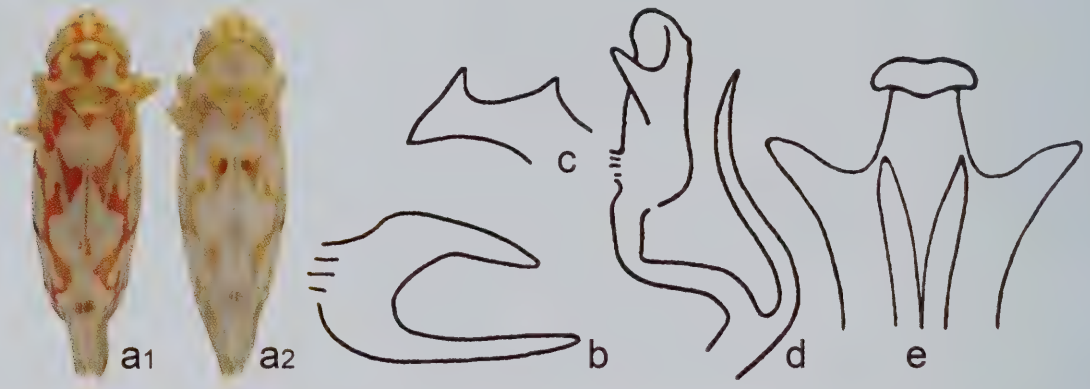
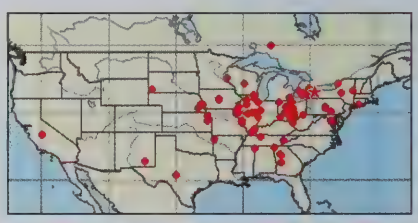


Figure 37. *E. delicata* McAtee. a2 – var. *accepta*. b, d, e – from Beamer 1938; c – from Hepner, unpublished.

38. ***Erythroneura vitifex*** Fitch, 1856 (Fig. 38)
Erythroneura vitifex Fitch, 1856:392
Erythroneura vitifex Beamer, 1938:281, neotype designation
Erythroneura vitifix Padley, 1941:395, missp.



Description: Length 2.7–3 mm. Abdomen. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe angulate; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex longer than third; third point short; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, broad in lateral view, round in crossection, with dorsal carina; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes subapical, triangular. Dorsum yellow or white, with red or orange color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum pale, with reddish lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewing with oblique vittae forming continuous zigzag pattern; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Neotype ♂, Canada, Ontario, Vineland, VIII 1922, (Robinson), (KSEM).
Distribution: USA, southern Canada.
Host plants: *Vitis* spp.

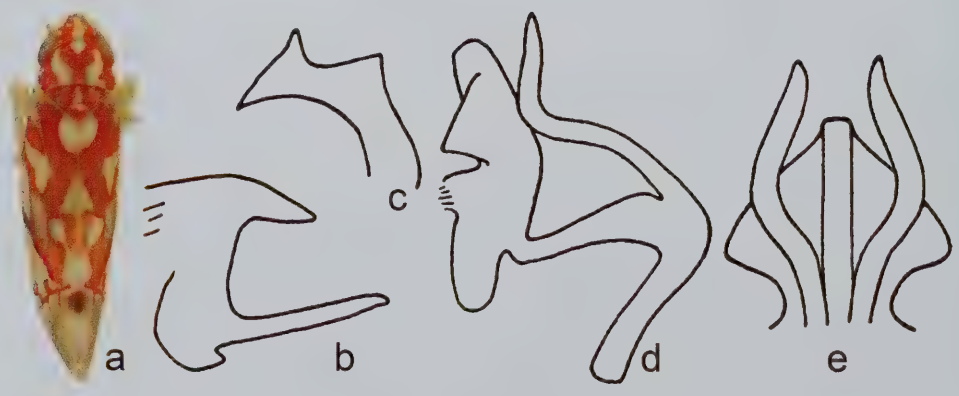
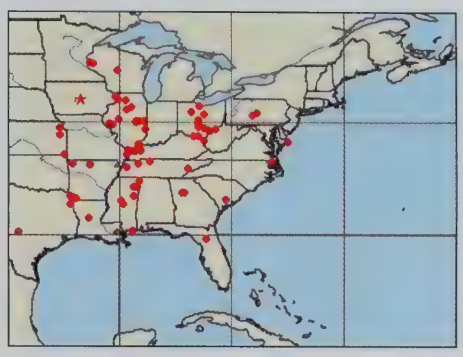


Figure 38. *E. vitifex* Fitch. b–e – from Beamer 1938.

39. ***Erythroneura rubra*** (Gillette, 1898) (Fig. 39)
Typhlocyba comes var. *rubra* Gillette, 1898:764
Erythroneura comes var. *rubra* Van Duzee, 1916:77
Erythroneura irrorata Robinson, 1924b:154
Erythroneura rubra Robinson, 1926:135



Description: Length 2.9–3.1 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe angulate; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point subequal in size with second; angle between basal and third points about 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, broad in lateral view, round in crossection, with dorsal carina, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes subapical, triangular. Dorsum yellow or white, with strongly developed reddish color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y- or V-shaped medial vitta; mesonotum entirely red; thoracic venter entirely dark; forewings with oblique vittae forming zigzag pattern; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell without brown spot.
Type locality: Holotype ♀, USA, Iowa, (Baker), (USNM).
Distribution: Central and eastern USA.
Host plants: *Vitis* spp.

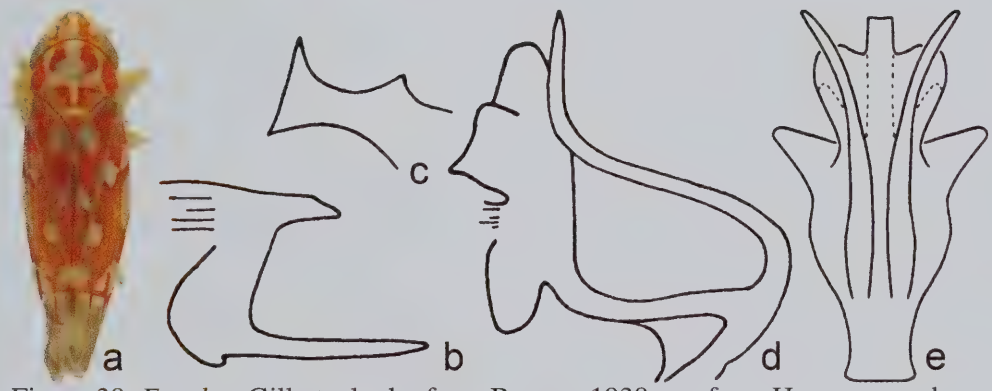
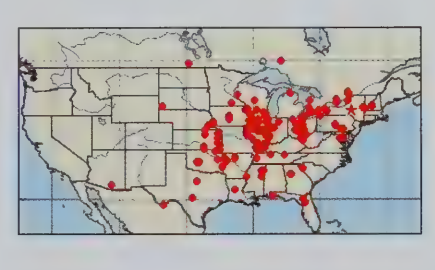


Figure 39. *E. rubra* Gillette. b, d – from Beamer 1938; c – from Hepner, unpublished

40. ***Erythroneura vitis*** (Harris, 1831) (Fig. 40)
Tettigonia vitis Harris, 1831:43
Erythroneura vitis Fitch, 1851:63
Erythroneura vitis var. *corona* McAtee, 1920:304, **syn.n.**
Erythroneura comes var. *venusta* McAtee, 1920:319
Erythroneura vitis var. *flava* Robinson, 1924a:62
Grapevine leafhopper



Description: Length 2.8–3.1 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Second point of style apex longer than third; third point shorter than second; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, broad in lateral view, round in crossection, with dorsal carina, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes apical, triangular. Coloration strongly varies; dorsum yellow or white, with reddish brown color pattern; vertex unicolorous pale or with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y- or V-shaped medial vitta or almost entirely dark; mesonotum entirely dark; thoracic venter with dark mesosternum, remainder pale; forewing with two pale

crossbands of various width; dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.
Type locality: Holotype [sex unknown], USA, New York, (Harris), (BSNH). Type was not studied.
Distribution: Eastern and southwestern USA, southeastern Canada.
Host plant: *Vitis* spp.

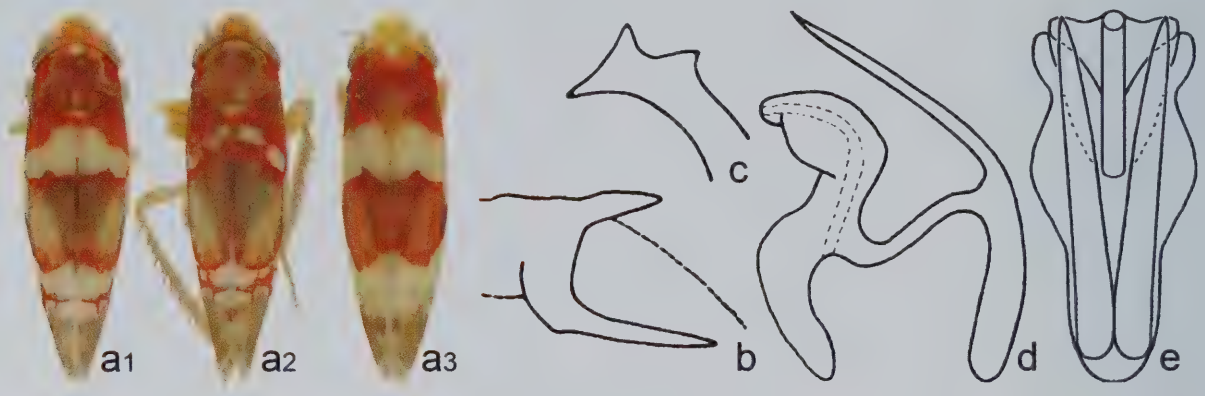
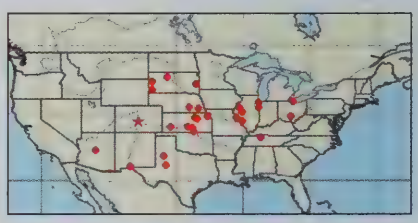


Figure 40. *E. vitis* Harris. a2 – var. *corona*; a3 – var. *flava*; b, c – from Beamer 1938; d – from Hepner, unpublished.

41. ***Erythroneura coloradensis*** (Gillette, 1892) (Fig. 41)



Typhlocyba vitifex var. *coloradoensis* Gillette, 1892:16
Typhlocyba vitifex var. *coloradensis* Gillette & Baker, 1895:113, emend.
Erythroneura comes var. *coloradensis* Van Duzee, 1914:57
Typhlocyba celoradensis Merrill, 1915:21, missp.
Typhlocyba colorado Gillette & List, 1921:20, missp.
Erythroneura coloradensis Robinson, 1926:134
Erythroneura coloradensis Beamer, 1938:278, lectotype designation

Description: Length 2.8–3.2 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point of style apex not longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft curved dorsally, broad in lateral view, round in crossection, with dorsal carina, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes apical, triangular. Dorsum yellow or white, with reddish or orange color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y- or V-shaped medial vitta; mesonotum pale, with black lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Lectotype ♂, USA, Colorado, (Gillette), (USNM).
Distribution: Central and southwestern USA, southeastern Canada.
Host plants: *Vitis* spp.

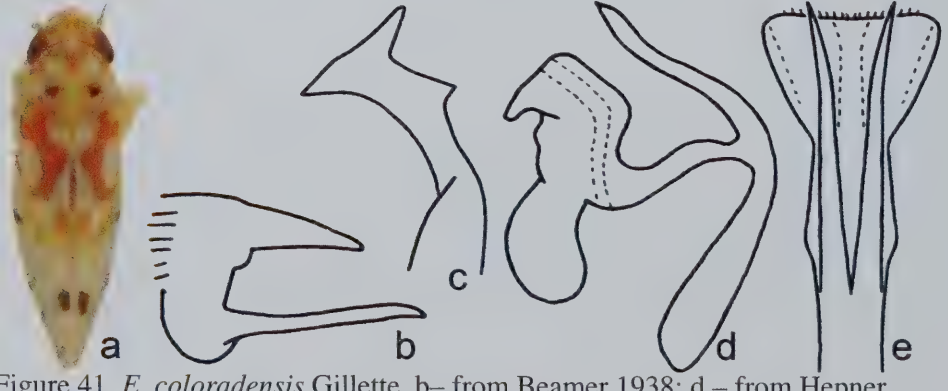
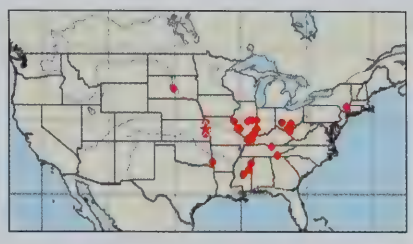


Figure 41. *E. coloradensis* Gillette. b– from Beamer 1938; d – from Hepner, unpublished.

42. ***Erythroneura fraxa*** Robinson, 1924 (Fig. 42)
Erythroneura fraxa Robinson, 1924c:292



Description: Length 2.9–3.2 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point not longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft straight in lateral view, slender in lateral view, round in crossection, with distinct apical spicules; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes apical, triangular. Dorsum yellow or white, with orange or red color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum pale, with reddish lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewing with oblique vittae usully forming continuous zigzag pattern; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype ♀, USA, Kansas, Douglas Co., XII 1923, (Robinson), (KSEM).
Distribution: Central and eastern USA.
Host plants: *Cercis canadensis*.

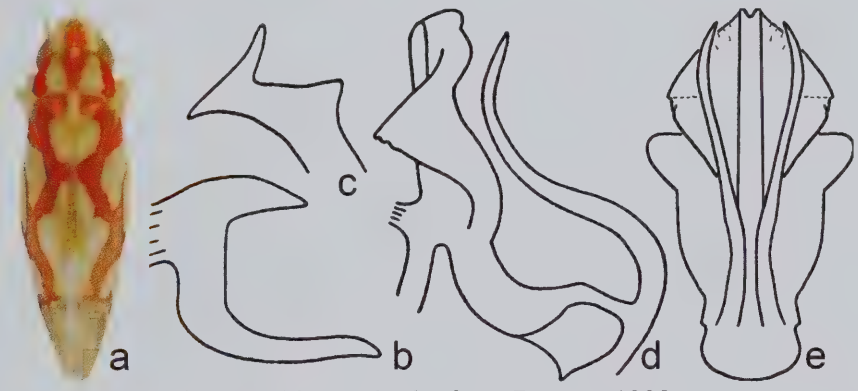
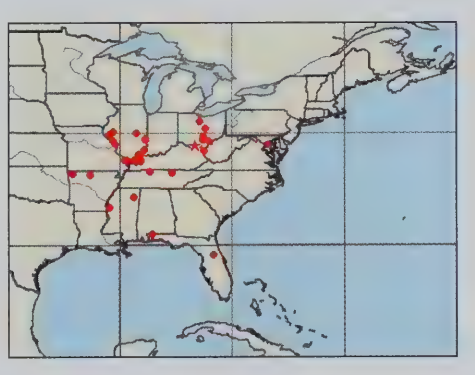


Figure 42. *E. fraxa* Robinson. b–d – from Beamer 1938.

43. ***Erythroneura vaga*** Johnson, 1934 (Fig. 43)
Erythroneura vaga Johnson, 1934:260



Description: Length 2.9–3.1 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point elongate, longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium shorter than shaft; shaft curved dorsally, slender in lateral view, round in crossection, with unpaired process on dorsal apodeme; ventral processes placed basally, close to shaft, shorter than shaft, parallel to each other on ventral side of aedeagus; distal processes apical, slender. Coloration similar to *E. comes* Say.
Type locality: Holotype♂, USA, Ohio, Adams Co., Mineral Springs, 31 VIII 1931 (Osborn), (OSU).
Distribution: Central and eastern USA.
Host plants: *Cercis canadensis*.
Note: *E. vaga* sensu Beamer, 1938a equals *E. kerzhneri* sp.n.

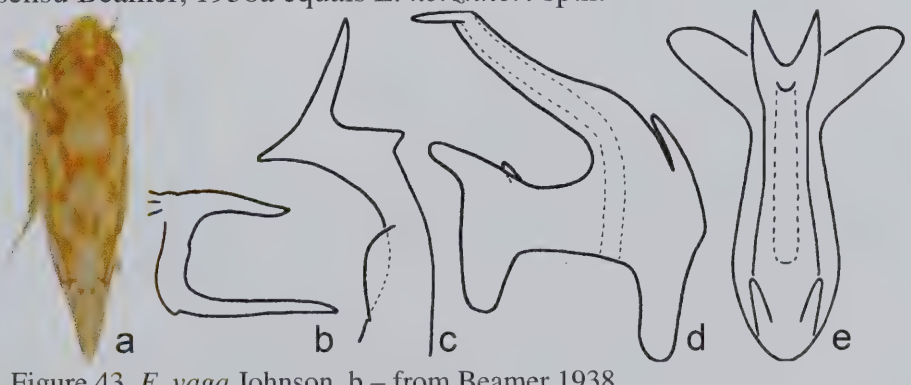
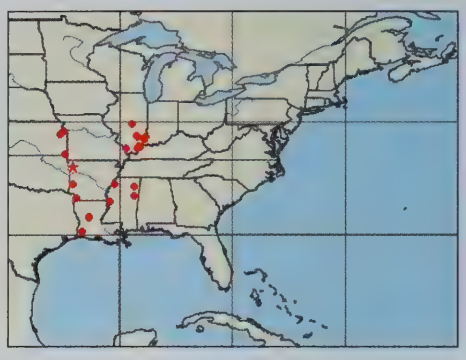


Figure 43. *E. vaga* Johnson. b – from Beamer 1938.

44. ***Erythroneura kerzhneri*** Dmitriev & Dietrich **sp.n.** (Fig. 44)
Erythroneura vaga Beamer, 1938:285 not Johnson, 1934, misid.



Description: Length 2.8–3.1 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex well developed; third point elongate, about as long as distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium shorter than shaft; shaft symmetrical, curved ventrally, slender in lateral view, smooth or denticulate distally, round in crossection; with pair of long dorsal processes between shaft and dorsal apodeme; apex of aedeagus broadened in ventral view; ventral processes placed basally, well separated from shaft, shorter than shaft, parallel to each other on ventral side of aedeagus, simple or bifurcated at apex; distal processes short, apical. Coloration similar to that of *E. kennedyi* Knull; dorsum yellow or white, with reddish or orange color pattern; vertex with orange parallel submedial lines (often with lateral branch), midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum pale, with reddish lateral triangles; thoracic venter entirely pale; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Diagnosis: *E. kerzhneri* sp.n. is similar to *E. kennedyi* Knull, but has the dorsal and distal processes of the aedeagus much shorter, the basal processes longer, and the third point of the style longer, about as long as distance between other points.
Type locality: Holotype ♂, USA, Arkansas, Washington Co., 30 VI 1940 (Sanderson), (KSEM).
Studied material: Paratypes: USA, 2 ♂, Arkansas, Miller Co., Fouke, 21 XII 1931 (Beamer), (KSEM); 2 ♂, Arkansas, Polk Co., 21 VIII 1928 (Beamer), (KSEM); 2 ♂, Illinois, Clay Co., 31 III 1929 (Oman), (KSEM); 1 ♂, Illinois, Clay Co., 31 III 1929 (Beamer), (KSEM); 8 ♂, Illinois, Clay Co., Flora, 31 III 1929 (Beamer), (KSEM). Other studied material from Illinois, Kansas, Louisiana, and Mississippi excluded from paratypes.
Distribution: Central and southeastern USA.
Host plants: *Ilex decidua, Ulmus alata.*
Note: The species named in honor of Prof. Izyaslav Kerzhner (Zoological Institute, Russian Academy of Sciences, St. Petersburg), Russian specialist on Heteroptera.

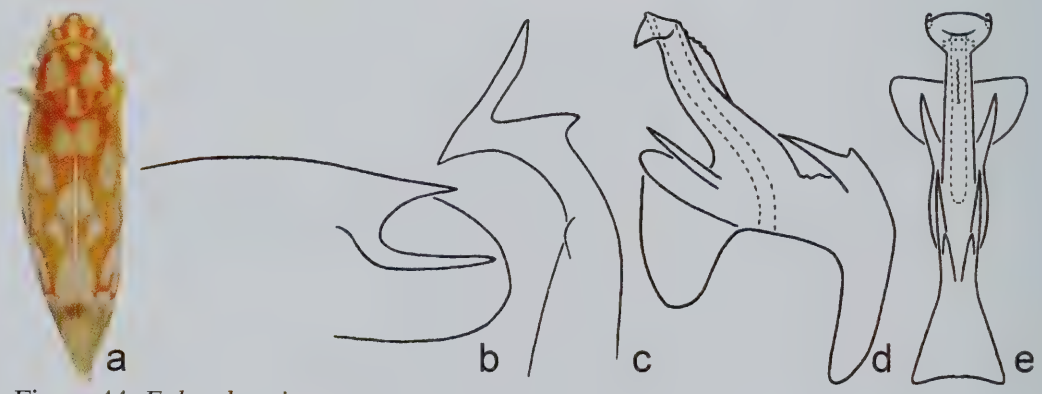
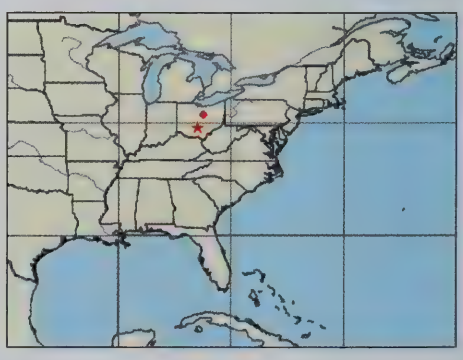


Figure 44. *E. kerzhneri* sp.n.

45. ***Erythroneura kennedyi*** Knull, 1945 (Fig. 45)
Erythroneura kennedyi Knull, 1945:109



Description: Length 2.9–3.1 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex longer than third; third point not longer than half distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium shorter than

shaft of aedeagus; shaft straight and slender in lateral view, round in crossection; with long dorsal processes between shaft and dorsal apodeme; ventral processes placed basally, close to shaft, shorter than shaft, parallel to each other on ventral side; aedeagus distal processes apical, slender. Dorsum yellow or white, with reddish or orange color pattern; vertex with parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum pale, with reddish lateral triangles; thoracic venter entirely pale; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype ♂, USA, Ohio, Pickaway Co., 20 II 1934 (Caldwell), (OSU).
Distribution: Known only from type locality in Ohio.
Host plants: Unknown.

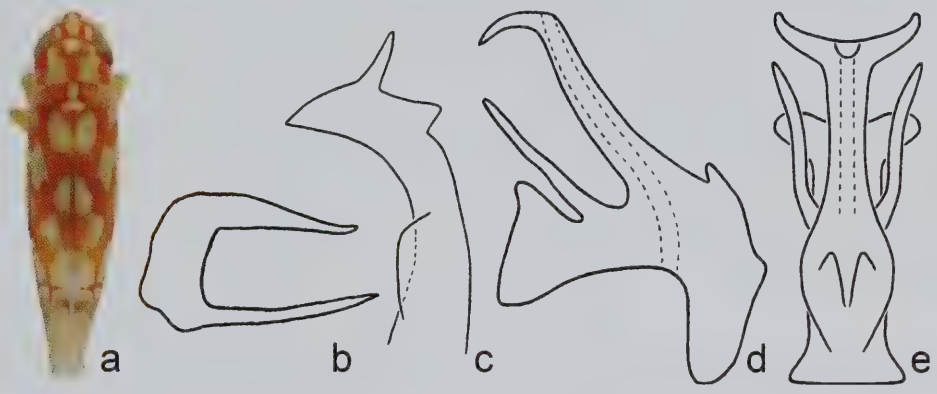


Figure 45. *E. kennedyi* Knull. b – from Knull 1945.

46. ***Erythroneura ancora*** Beamer, 1929 (Fig. 46)
Erythroneura ancora Beamer, 1929:122

Description: Length 3.1–3.2 mm. Male genitalia. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex longer than third; third point short; angle between basal and third points about 90°. Aedeagus with preatrium shorter than shaft; shaft curved dorsally, slender in lateral view, with small dorsal distal lobe; ventral processes placed basally, close to shaft, shorter than shaft; distal processes absent. Dorsum yellow, with orange color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum pale, with dark lateral triangles; thoracic venter entirely pale; forewings with oblique vittae usully forming zigzag pattern; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype, ♂, USA, Texas, Culberson Co., 10 VII 1927 (Beamer), (KSEM).
Distribution: Known only from type locality in Texas.
Host plants: Unknown.

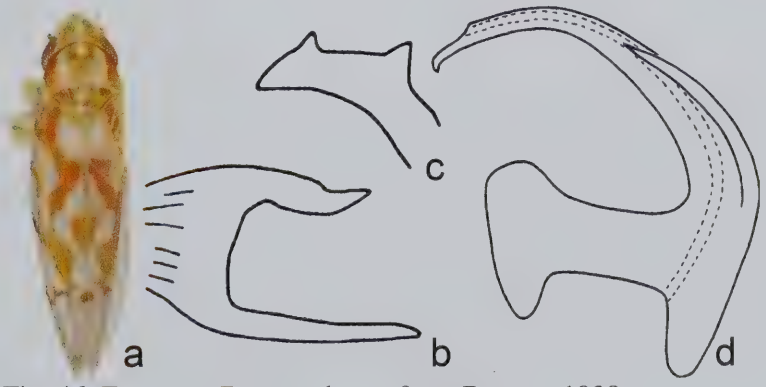


Fig. 46. E. ancora Beamer. b, c – from Beamer 1938.

47. ***Erythroneura tacita*** Beamer, 1938 (Fig. 47)

Erythroneura tacita Beamer, 1938:293

Description: Length 3.1–3.5 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, dorsal branch strongly reduced, ventral branch much longer. Second point of style apex longer than third; third point very short; angle between basal and third points about 90°. Aedeagus with preatrium about as long as shaft; shaft curved dorsally, slender in lateral view, round in crossection; ventral processes placed basally, well separated from shaft, shorter than shaft, evenly divergent; distal processes long, slender. Dorsum yellow or white, with reddish or orange color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y-shaped medial vitta; mesonotum entirely pale; thoracic venter entirely pale; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.

Type locality: Holotype ♂, USA, Washington, Ferry Co., Republic, 6 VIII 1931 (Beamer), (KSEM).

Distribution: Western USA, southwestern Canada.

Host plants: Unknown.

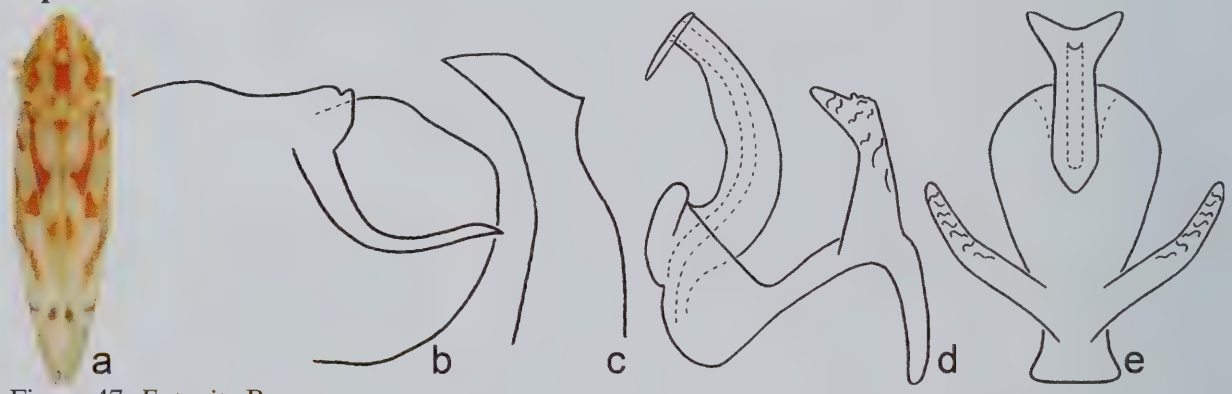
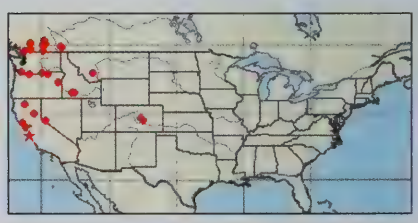


Figure 47. *E. tacita* Beamer.

48. ***Erythroneura caetra*** McAtee, 1924 (Fig. 48)



Erythroneura ligata var. *caetra* McAtee, 1924b:130

Erythroneura ligata var. *caestra* DeLong & Caldwell, 1937:79, missp.

Erythroneura caetra Beamer, 1938:281

Description: Length 2.9–3.3 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe angulate; dorsal appendages extended beyond pygofer apex, C-shaped, ventral branch much longer than dorsal. Second point of style apex longer than third; third point of style apex very short or absent. Aedeagus with preatrium shorter than shaft; shaft curved dorsally, broad in lateral view, compressed in crossection, with subapical dorsal lobe, with distinct apical spicules; ventral processes placed basally, well separated from shaft, shorter than shaft, parallel to each other on ventral side of aedeagus; distal processes apical, small, toothlike. Dorsum yellow or white with reddish brown color; vertex with parallel submedial lines, midline pale; anteclypeus dark; pronotum dark with pale lateral margins; mesonotum pale, with black lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewings with oblique vittae forming continuous zigzag pattern; clavus with continuous vitta parallel to suture; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.

Type locality: Holotype ♀, USA, California, Monterey Co., Salinas, 26 IV 1908 (Ball), (USNM).

Distribution: Western USA, southwestern Canada.

Host plants: *Salix exigua*.

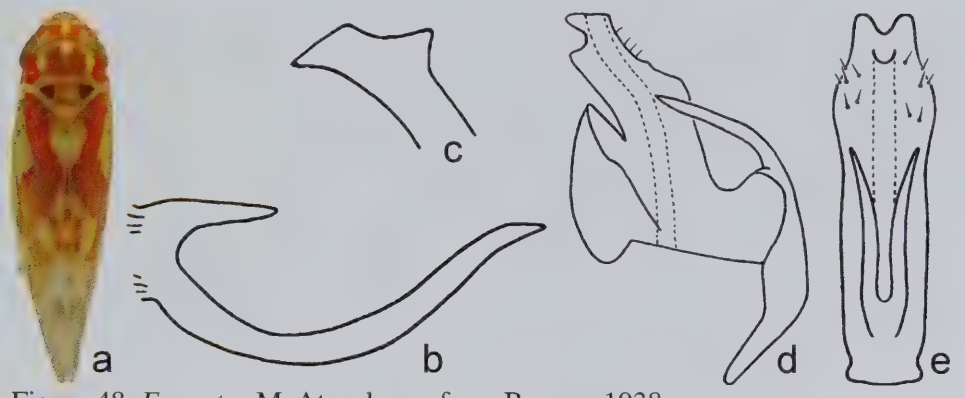
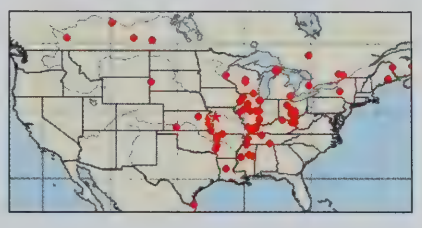


Figure 48. *E. caetra* McAtee. b, c – from Beamer 1938.

49. ***Erythroneura rosa*** Robinson, 1924 (Fig. 49)
Erythroneura rosa Robinson, 1924a:58
Erythroneura mallochi McAtee, 1924c:41
Erythroneura repetita McAtee, 1926:131, **syn.n.**



Description: Length 2.8–3.2 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe angulate; dorsal appendages extended beyond pygofer apex, C-shaped, ventral branch much longer than dorsal, branches strongly divergent. Second point of style apex longer than third; third point very short or absent. Aedeagus with preatrium shorter than shaft; shaft curved dorsally, broad in lateral view, compressed in crossection, with subapical dorsal lobe, with distinct apical spicules; ventral processes placed basally, well separated from shaft, shorter than shaft, parallel to each other on ventral side of aedeagus; distal processes apical, small tooth-like. Dorsum yellow or white, with reddish or brownish color pattern; vertex with orange parallel submedial lines, midline pale; anteclypeus dark; pronotum dark with pale lateral margins or pale with two longitudinal strips; mesonotum pale, with dark lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewings with oblique vittae forming zigzag pattern or dark with two narrow crossbands; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.

Type locality: Holotype ♂, USA, Missouri, Jackson Co., Atherton, 19 V 1922 (Adams), (KSEM).

Distribution: Central and eastern USA, southern Canada.

Host plants: *Salix myricoides, S. babylonica, S. cordata, S. bebbiana, S. petiolaris, S. caprea, S. humilis, S. interior.*

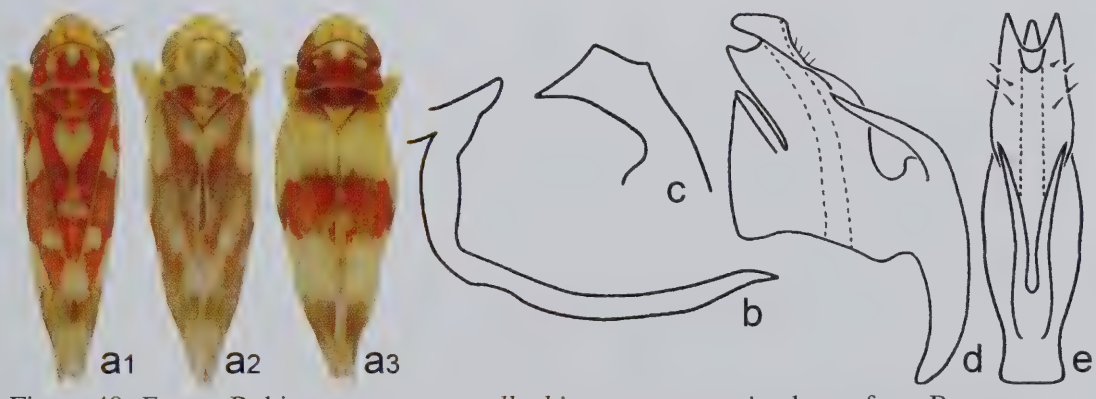
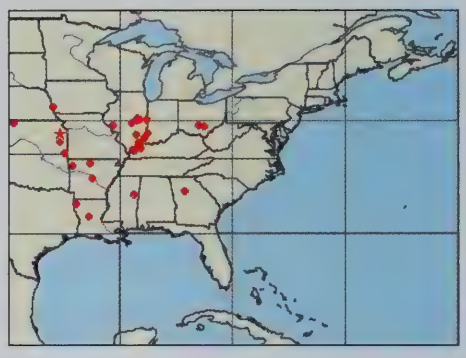


Figure 49. *E. rosa* Robinson. a_2 – var. *mallochi;* a_3 – var. *repetita*; b, c – from Beamer 1938.

50. ***Erythroneura omaska*** Robinson, 1924 (Fig.50)
Erythroneura omaska Robinson, 1924a:62



Description: Length 3–3.2 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, C-shaped, branches subequal in length. Second point of style apex longer than third; third point short; angle between basal and third points about 90°. Aedeagus with preatrium shorter than shaft; shaft curved dorsally, slender in lateral view, denticulate distally, depressed in crossection. Aedeagus with two dorsal processes arising near midlength of shaft; ventral processes absent; distal processes apical, slender. Dorsum yellow or white, with reddish or orange color pattern; vertex with parallel submedial lines, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with Y- or V-shaped medial vitta; mesonotum pale, with orange lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II with distal spot; inner apical cell with brown spot basally.
Type locality: Holotype ♂, USA, Kansas, Douglas Co., X 1923, (Robinson), (KSEM).
Distribution: Central and eastern USA.
Host plants: Unknown. Recorded from *Rubus* sp., *Vitis* sp., *Ilex decidua*.

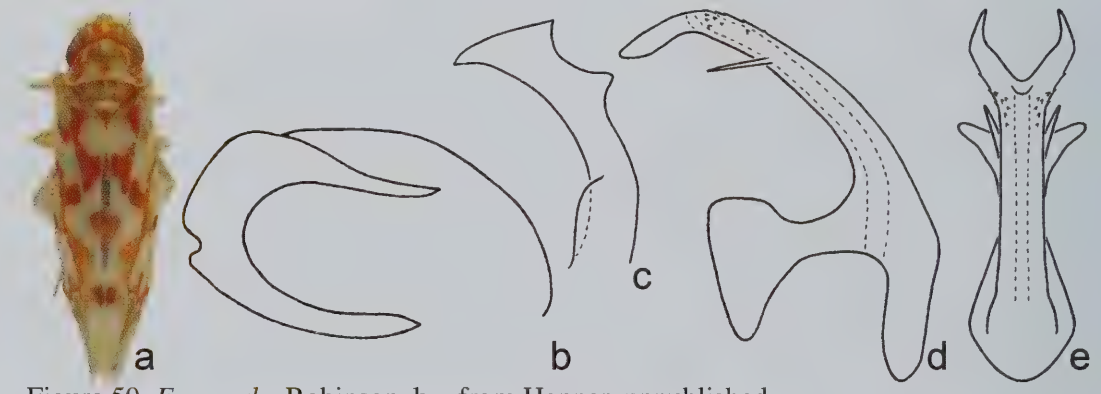
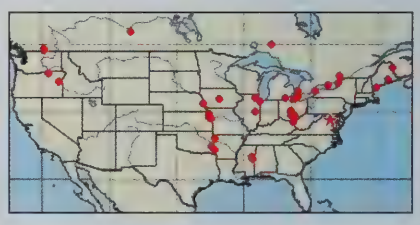


Figure 50. *E. omaska* Robinson. b – from Hepner, unpublished.

51. ***Erythroneura rubrella*** McAtee, 1920 (Fig. 51)
Erythroneura comes var. *rubrella* McAtee, 1920:316
Erythroneura rubrella Johnson, 1935:109



Description: Length 2.7–3 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe angulate; dorsal appendages extended beyond pygofer apex, C-shaped, ventral branch much longer than dorsal. Second point of style apex very short, tooth like; third point of style apex subequal in size with second; angle between basal and third points about 90°. Aedeagus with preatrium shorter than shaft; shaft straight and broad in lateral view, compressed in crossection, with dorsal keel; apex of aedeagus acuminate in ventral view, with distinct apical spicules; ventral processes absent; distal processes absent. Dorsum yellow or white, with reddish color pattern; vertex with orange parallel submedial lines, midline red; anteclypeus dark; pronotum dark with pale lateral margins or pale with two longitudinal strips; mesonotum pale, with reddish lateral triangles; thoracic venter entirely dark; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.
Type locality: Holotype ♂, USA, Maryland, Montgomery Co., Plummers Island, 30 XI 1913 (McAtee), (USNM).
Distribution: Northwestern, central, and eastern USA, southern Canada.
Host plants: *Cornus pumila, C. stolonifera*.

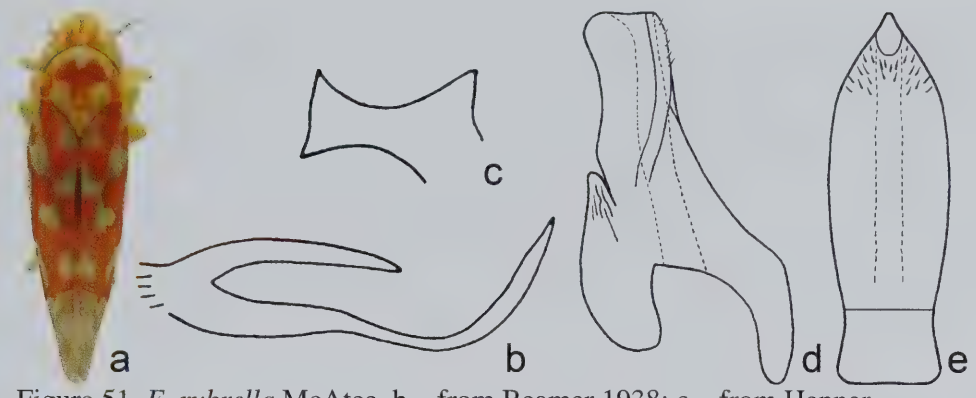
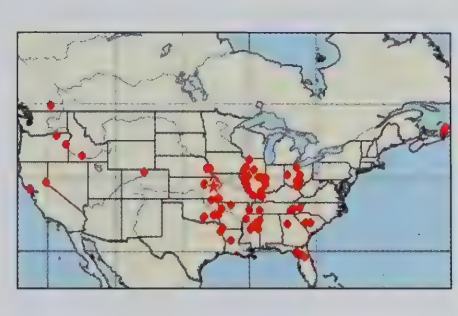


Figure 51. *E. rubrella* McAtee. b – from Beamer 1938; c – from Hepner, unpublished.

52. ***Erythroneura corni*** Robinson, 1924 (Fig. 52)
Erythroneura corni Robinson, 1924a:60
Erythroneura ornata Osborn, 1928b:364



Description: Length 2.6–3 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages extended beyond pygofer apex, C-shaped, branches very long of subequal length. Second point of style apex very short, tooth like; third point not longer than half distance between other two points; angle between basal and third points about 90°. Aedeagus with preatrium shorter than shaft; shaft curved dorsally, slender in lateral view, compressed in crossection, with long dorsal distal lobe; apex acuminate in ventral view, with distinct apical spicules. Aedeagus without processes. Dorsum yellow or white, with orange or red color pattern; vertex with parallel submedial lines, midline red; anteclypeus dark; pronotum dark with pale lateral margins or pale with two longitudinal strips; mesonotum pale, with reddish lateral triangles; thoracic venter entirely dark; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.
Type locality: Holotype ♂, USA, Kansas, Douglas Co., X 1923, (Robinson), (KSEM).
Distribution: USA, southern Canada.
Host plants: *Cornus* spp.

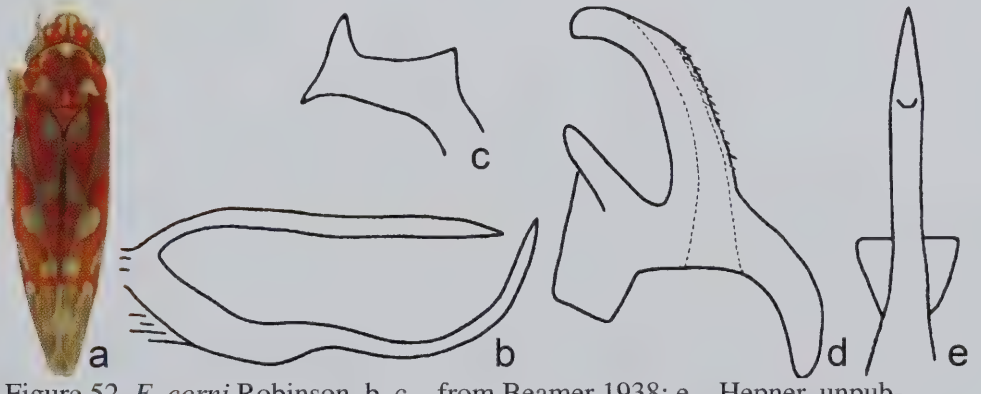
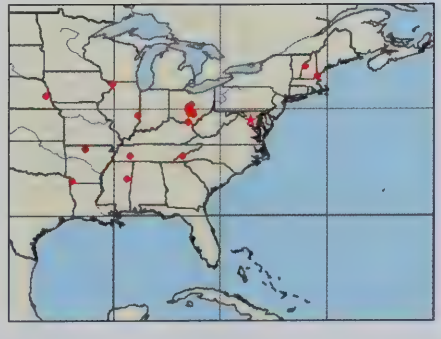


Figure 52. *E. corni* Robinson. b, c – from Beamer 1938; e – Hepner, unpublished.

53. ***Erythroneura bidens*** McAtee, 1924 (Fig. 53)
Erythroneura comes var. *bidens* McAtee, 1924a:39
Erythroneura comes var. *suffusa* McAtee, 1924a:39
Erythroneura bidens Beamer, 1938:287



Description: Length 2.8–3.2 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages extended beyond pygofer apex, C-shaped;

ventral branch about twice as long as dorsal, twisted and extended at apex. Second point of style apex very short, tooth like; third point subequal in size with second; angle between basal and third points about 90°. Aedeagus with preatrium shorter than shaft; shaft straight and slender in lateral view, compressed in crossection, with long dorsal distal lobe; apex acuminate in ventral view, with distinct apical spicules. Aedeagus without processes. Dorsum yellow or white, with reddish or orange color pattern; vertex with parallel submedial lines, midline red; anteclypeus dark; pronotum dark with pale lateral margins or pale with two longitudinal strips; mesonotum pale, with reddish lateral triangles; thoracic venter entirely dark; forewing with broken oblique vittae; clavus with separate basal and distal vittae; dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.

Type locality: Holotype ♀, USA, Virginia, Fairfax Co., Scotts Run Nature Preserve, Stubblefield Falls, on *Pinus virginiana*, 23 X 1921 (Malloch), (USNM).

Distribution: Central and eastern USA.

Host plants: *Cornus* spp.

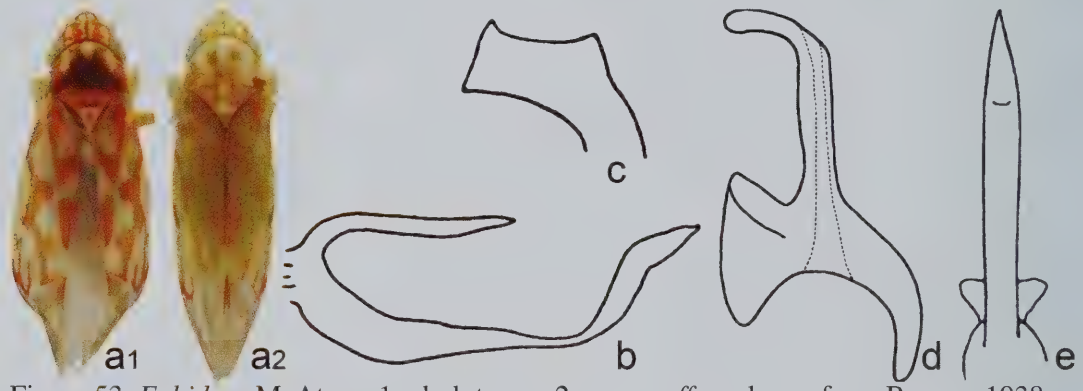
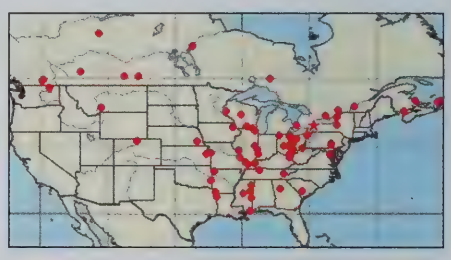


Figure 53. *E. bidens* McAtee. a1 – holotype; a2 – var. *suffusa*. b, c – from Beamer 1938; e – from Hepner, unpublished.

54. ***Erythroneura ontari*** Robinson, 1924 (Fig. 54)

Erythroneura ontari Robinson, 1924a:60



Description: Length 2.5–2.8 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages extended beyond pygofer apex, C-shaped; ventral branch about twice as long as dorsal. Second point of style apex very short, tooth like; third point subequal in size with second; angle between basal and third points about 90°. Aedeagus with preatrium shorter than shaft; shaft straight and slender in lateral view, compressed in crossection, with long dorsal distal lobe; apex acuminate in ventral view, with distinct apical spicules. Aedeagus without processes. Coloration similar to *E. corni* Robinson.

Type locality: Holotype ♂, Canada, Ontario, Vineland, I 1923, (Robinson), (KSEM).

Distribution: Northwestern, central, and eastern USA, southern Canada.

Host plants: *Cornus* spp.

Note: *E. ontari* Robinson may be a variant of *E. corni* Robinson rather than a distinct species. They are often collected together and differ primarily in the length of the dorsal branch of the pygofer process. However, intermediate forms were not found.

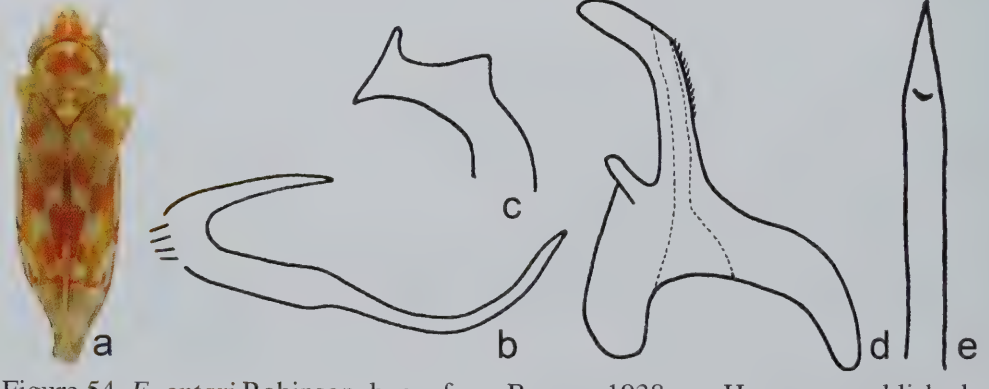


Figure 54. *E. ontari* Robinson. b, c – from Beamer 1938; e – Hepner, unpublished.

Genus ***Erasmoneura*** Young, 1952

Erythroneura (*Erasmoneura*) Young, 1952:80 (Type: *Erythroneura vulnerata Fitch*, 1851)

Erasmoneura Dietrich & Dmitriev, 2006:139

Description: Length 2.2–3.4 mm, relatively slender. Head narrower than pronotum; crown fore margin strongly produced and angulate medially; ocelli absent or vestigial. Face depressed in profile, less than 45° from horizontal; anteclypeus narrow in both sexes. Forewing outer apical cell short, less than 2X longer than width or about 2X as long as wide; second apical cell quadrate (ir crossvein present); third apical cell parallel sided, straight; CuP shorter than segment of CuA between Cu and MP; basal segment of MP shorter than basal segment of CuA; inner apical cell with distinctly angulate base; Pcu not visible. Hindwing with truncate apex; submarginal vein not extended to wing apex; RA present; MP and CuA fused for short distance or separated by m-cu crossvein, convergent distally. Front femur AV row with one basal seta distinctly larger than others; PV row without fine basal setae. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer apex not extended to apex of subgenital plate; dorsal emargination extended to base of segment; basolateral setae in distinct group, small; distal setae undifferentiated; long fine setae present or absent; apex with rigid setae on internal surface. Pygofer dorsal appendage movably articulated, or at least with distinct basal suture separating it from lobe; simple or bifurcate; ventral appendage absent. Subgenital plates free; lateral margin with angulate subbasal projection; section basad of medial constriction shorter than distal section; with 4 basal macrosetae, uniseriate along margin; marginal short rigid setae forming continuous row. Style preapical lobe prominent; apex with 3 points. Aedeagus articulated to connective; dorsal apodeme broadly expanded in lateral view, with distinct V-shaped ligaments connected to pygofer appendages; shaft symmetrical, with processes. Connective median anterior lobe absent; arms long; stem well developed, depressed. Anal tube without processes. Coloration variable.

Distribution: North America; *E. vulnerata* Fitch recently established in northern Italy (Duso at al., 2005).

Host plants: *Vitis* spp. and herbs.

Key to Species of the Genus *Erasmoneura*[1]

1. Aedeagus shaft very short, with ventral processes; processes as long as or longer than shaft; without distal processes (Fig. 55e). Pygofer with dorsal appendage bifurcate (Figs. 55b, 56b). 2

1'. Aedeagus shaft long, without ventral processes, with distal processes (Fig. 58e). Pygofer with dorsal appendage not bifurcate (Fig. 58b). 4

2(1). Pygofer dorsal appendage bifurcate far from base, branches very short; dorsal branch slightly curved upward (Fig. 55b). ..... 55. **E. vulnerata** Fitch

2'. Pygofer dorsal appendage bifurcate closer to base, branches longer than basal part of appendage; dorsal branch straight or curved downward (Figs. 56b, 57b). 3

3(2). Branches of pygofer appendage subequal in length (Fig. 56b). ..... 56. **E. fulmina** McAtee

3'. Dorsal branch of pygofer appendage about twice as long as ventral (Fig. 57b). ..... 57. **E. variabilis** Beamer

4(1). Third point of style apex shorter than half distance between other two points (Fig. 58c). ..... 58. **E. nigra** Gillette

4'. Third point of style apex longer than half distance between other two points (Fig. 60c). 5

5(4). Third point of style apex more than 2X longer than distance between other two points (Fig. 59c). ..... 59. **E. nigerrima** McAtee

5'. Third point of style apex as long or only slightly longer than distance between other two points (Fig. 60c). 6

6(5). Ground color of dorsum dark brown or black (Figs. 60a, 61a). 7

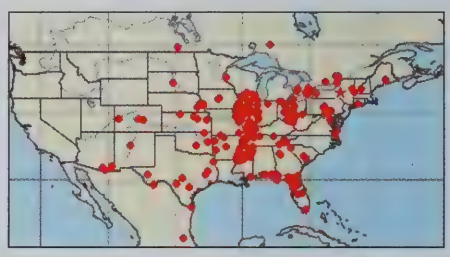
6'. Ground color of dorsum yellow, reddish, or light brown (Figs. 62a, 63a). 8

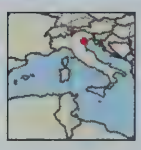
7(6). Aedeagus distal processes longer than dorsal distal lobe (Figs. 60d, 60e). Dorsum with pale spots (Fig. 60a). ..... 60. **E. atra** Johnson

[1] *E. bipentagona* Beamer, known only from the female holotype, is not included.

7'. Aedeagus distal processes not longer than dorsal distal lobe (Figs. 61d, 61e). Dorsum without pale spots (Fig. 61a). ..... 61. **E. caerula** Beamer
8(6). Aedeagus depressed in crossection, broad in ventral view (Figs. 62d, 62e). 9
8'. Aedeagus round in crossection, slender in ventral view (Figs. 64d, 64e). 10
9(8). Aedeagus distal processes directed basad in ventral view (Fig. 62e). Vertex pale; forewing yellow or pink (Fig. 62a). ..... 62. **E. rubricata** Van Duzee
9'. Aedeagus distal processes directed latarad in ventral view (Fig. 63e). Vertex and forewing reddish brown (Fig. 63a). ..... 63. **E. margaritae** sp.n.
10(8). Shaft of aedeagus curved dorsally in lateral view; dorsal distal lobe longer than distal processes (Fig. 64d). ..... 64. **E. emeljanovi** sp.n.
10'. Shaft of aedeagus curved ventrally in lateral view; dorsal distal lobe not longer than distal processes (Fig. 65d). ..... 65. **E. mixta** Beamer

55. ***Erasmoneura vulnerata*** (Fitch, 1851) (Fig. 55, Plate 1e)
Erythroneura vulnerata Fitch, 1851:62
Typhlocyba vulneata Lugger, 1896:61, missp.
Erythroneura gradata Robinson, 1924a:58, **syn.n.**
Erasmoneura vulnerata Dietrich & Dmitriev, 2006:140





Description: Length 2.7–3.2 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages bifurcate far from base, not extended beyond pygofer apex, curved upward. Second point of style apex very short, toothlike; third point elongate, not longer than half distance between other two points; angle between basal and third points about 90°. Aedeagus with preatrium longer than shaft; shaft very short membranous, straight and broad in lateral view, round in crossection; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at base, then parallel; distal processes absent. Dorsum white or yellow, with reddish or brownish color pattern; vertex mostly dark, with small pale spots, midline pale; anteclypeus brown; pronotum and mesonotum almost entirely dark; thoracic venter with dark mesosternum, remainder pale; forewing with reddish and brownish patches; clavus largely or entirely dark; dark spot at costal margin; apical cell II with distal spot; inner apical cell without brown spot.
Type locality: Holotype ♂, USA, New York, (NYSM).
Distribution: Central and eastern USA, southeastern Canada, northern Mexico, Italy (introduced, Duso et al., 2005).
Host plants: *Vitis* spp.

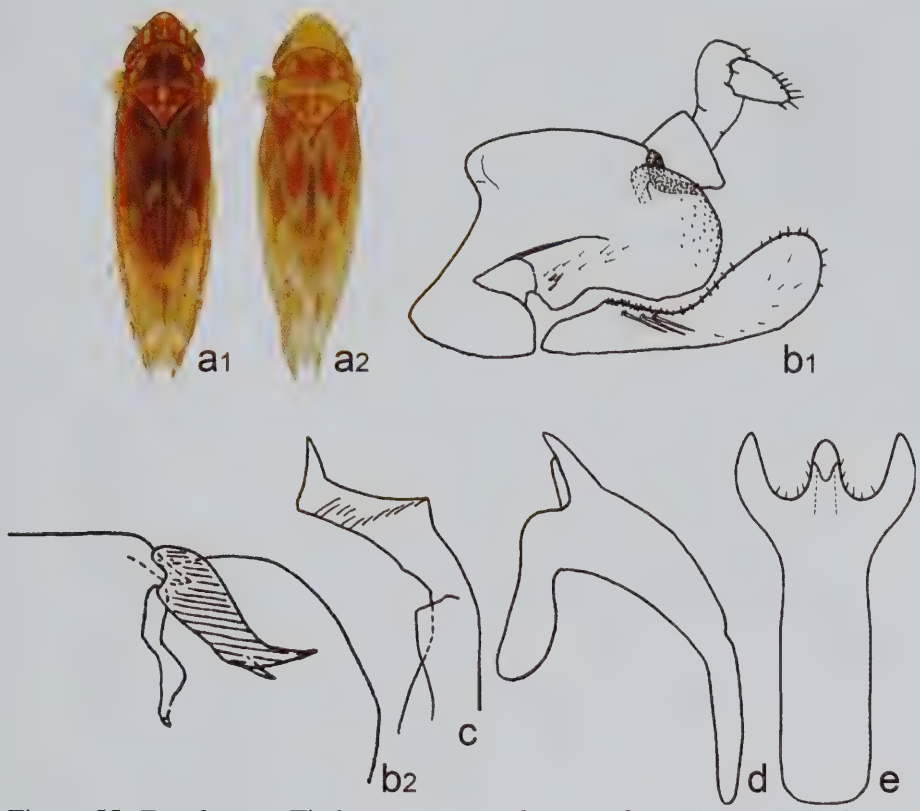
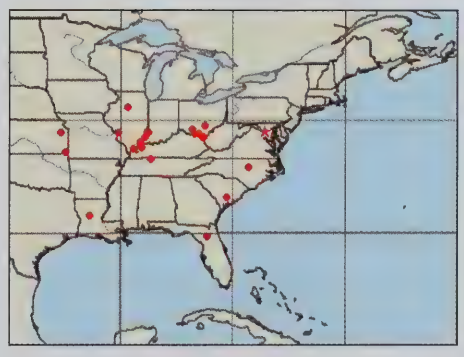


Figure 55. *E. vulnerata* Fitch. a2 – var. *gradata*. c – from Young 1952; b2 – from Ross 1965; b1 – from Dietrich & Dmitriev 2006.

56. ***Erasmoneura fulmina*** (McAtee, 1920) (Fig. 56)
Erythroneura vulnerata var. *fulmina* McAtee, 1920:274
Erythroneura pulchella Robinson, 1924b:155
Erythroneura bicolorata Beamer, 1937:11, **syn.n.**
Erythroneura fulmina Beamer, 1946:17
Erasmoneura fulmina Dietrich & Dmitriev, 2006:140



Description: Length 2.7–2.9 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages bifurcate near base, appendages parallel, not extended beyond pygofer apex, straight in lateral view. Second point of style apex very short, tooth like; third point elongate, longer than half distance between other two points; angle between basal and third points about 90°. Aedeagus with preatrium longer than shaft; shaft very short, membranous, straight and broad in lateral view, round in crossection; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at base, than parallel; distal processes absent. Dorsum yellow or white, with reddish or brownish color pattern; vertex mostly dark, with small pale spots, midline pale; anteclypeus dark; pronotum almost entirely dark; mesonotum pale, with dark lateral triangles or entirely dark; thoracic venter entirely dark. Forewing with reddish brown and pale patches, in some cases basal half much darker than distal half; dark spot at costal margin; apical cell II with distal spot; inner apical cell without brown spot.
Type locality: Holotype ♀, USA, Maryland, Montgomery Co., Plummers Island, 1 VI 1907 (Fisher), (USNM).
Distribution: Central and eastern USA.
Host plants: *Vitis* spp.

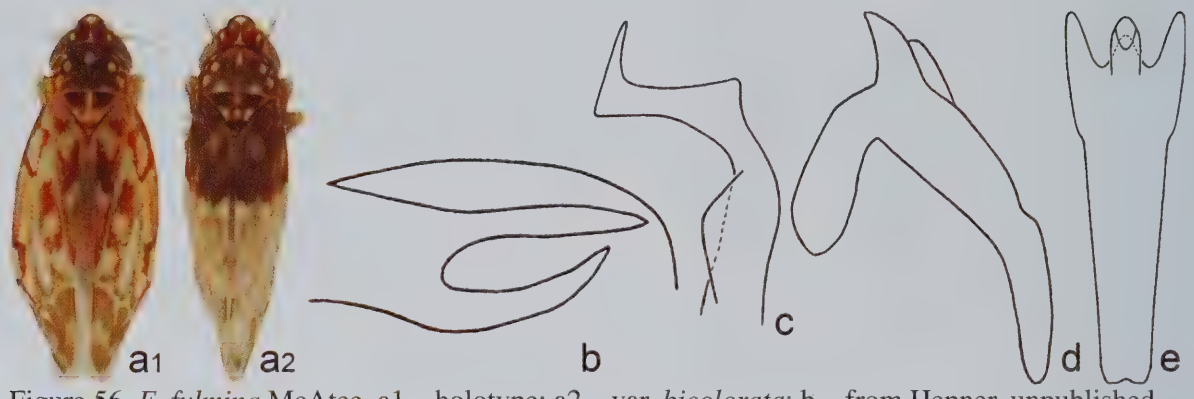
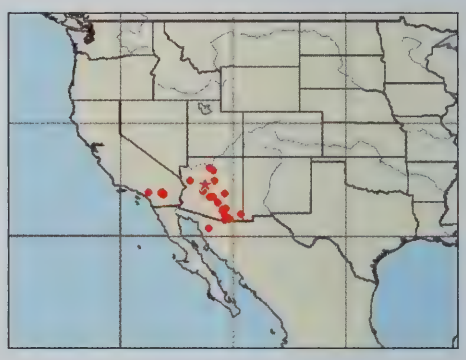


Figure 56. *E. fulmina* McAtee. a1 – holotype; a2 – var. *bicolorata*; b – from Hepner, unpublished.

57. ***Erasmoneura variabilis*** (Beamer, 1929) (Fig. 57)
Erythroneura variabilis Beamer, 1929:126
Erasmoneura variabilis Dietrich & Dmitriev, 2006:140
Variegated leafhopper



Description: Length 2.9–3.1 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages bifurcate near base, branches parallel to each other, not extended beyond pygofer apex. Second point of style apex very short, tooth like; third point elongate, not longer than half distance between other two points; angle between basal and third points about 90°. Aedeagus with preatrium longer than shaft; shaft very short, membranous, straight and broad in lateral view, round in crossection; ventral processes placed basally, well separated from shaft, longer than shaft, divergent at base, then parallel; distal processes absent. Coloration similar to *E. vulnerata* Fitch.
Type locality: Holotype ♂, USA, Arizona, Yavapai Co., 9 VIII 1927 (Beamer), (KSEM).
Distribution: Arizona, California, northern Mexico.
Host plants: *Vitis* spp.

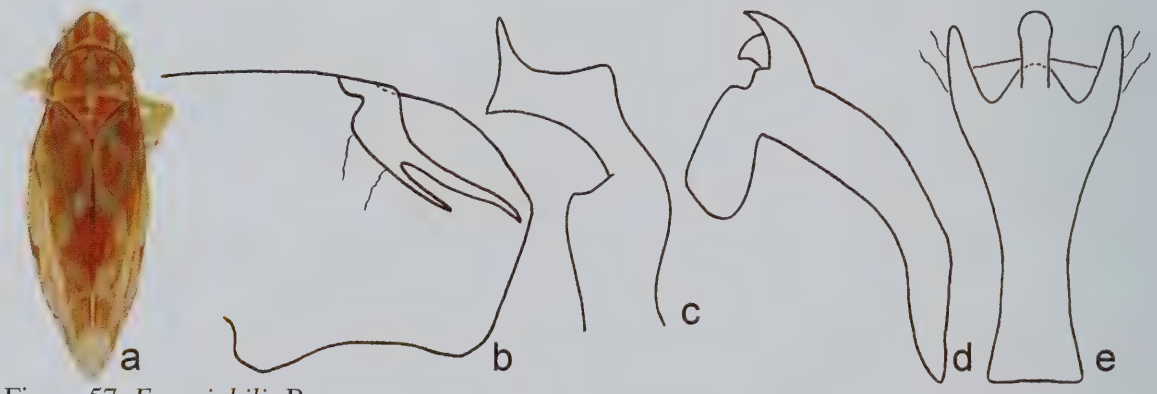
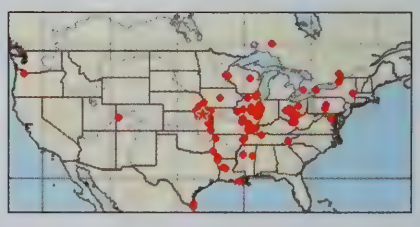


Figure 57. *E. variabilis* Beamer.

58. ***Erasmoneura nigra*** (Gillette, 1898) (Fig. 58, Plate 1f)
Typhlocyba vulnerata var. *niger* Gillette, 1898:765
Typhlocyba nigridorsum DeLong, 1916:110
Erythroneura niger Van Duzee, 1916:77
Erythroneura vulnerata var. *decora* McAtee, 1920:274, **syn.n.**
Erythroneura nigra Lawson, 1920:51
Erasmoneura nigra Dietrich & Dmitriev, 2006:140



Description: Length 2.7–3.1 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; pygofer dorsal appendages simple, not extended beyond pygofer apex,

slightly curved upward in lateral view. Second point of style apex very short, toothlike; third point elongate, not longer than half distance between other two points; angle between basal and third points about 90°. Aedeagus with preatrium about as long as shaft; shaft curved ventrally, broad in lateral view, round in crossection, with long dorsal distal lobe; ventral processes absent; distal processes long, subapical. Dorsum mostly black, with pale specks. Vertex mostly dark, midline pale; anteclypeus pale, concolorous with rest of face; pronotum with three pale specks at anterior margin; mesonotum almost entirely dark; thoracic venter with dark mesosternum, remainder pale. Forewing dark, with some pale specks and pale transverse veins.
Type locality: Holotype ♀, USA, Kansas, Pottawatomie Co., Onaga, (Crevecoeur), (USNM).
Distribution: USA, southern Canada.
Host plants: *Polygonum* spp.

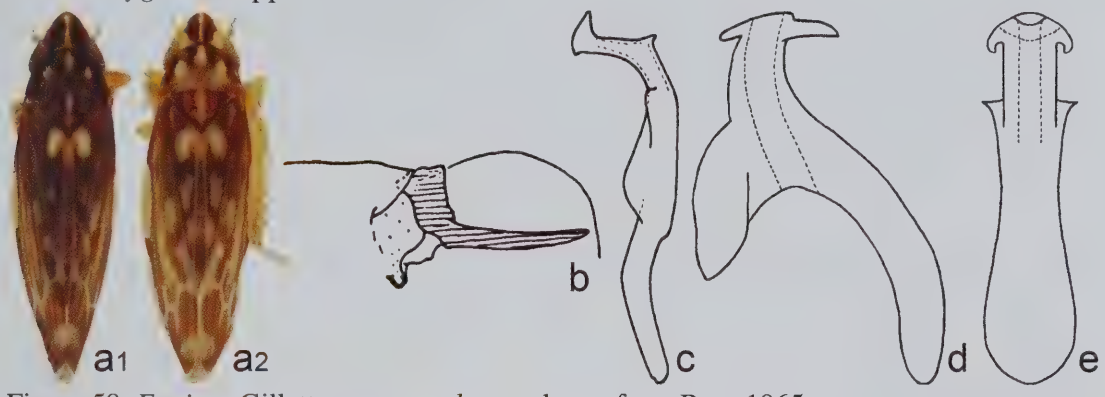
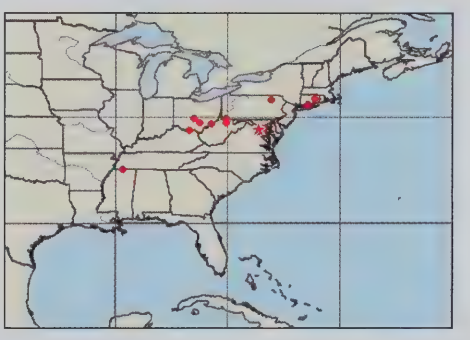


Figure 58. *E. nigra* Gillette. a2 – var. *decora*. b, c – from Ross 1965.

59. ***Erasmoneura nigerrima*** (McAtee, 1920) (Fig. 59)
Erythroneura vulnerata var. *nigerrima* McAtee, 1920:275
Erythroneura niger var. *nigerrima* Robinson, 1926:116
Erythroneura atrata Johnson, 1935:97, **syn.n.**
Erasmoneura nigerrima Dietrich & Dmitriev, 2006:140



Description: Length 2.2–2.5 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; pygofer dorsal appendages simple, movably articulated, extended beyond pygofer apex, curved downward in lateral view. Second point of style apex very short, tooth like; third point of style apex more than twice longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium longer than shaft; shaft curved ventrally, broad in lateral view; round in crossection, with subapical dorsal lobe; ventral processes absent; distal processes long, subapical. Dorsum black, with pale fore margin of vertex, pale specks on pronotum and mesonotum, and costal margins of wings, crossveins pale; usually with red spot at costal margin of forewing at level of crossveins; anteclypeus pale, concolorous with rest of face; thoracic venter with dark mesosternum, remainder pale.
Type locality: Holotype ♀, USA, Virginia, Alexandria Co., Maywood, 20 II 1916 (McAtee), (USNM).
Distribution: Central and northeastern USA.
Host plants: Unknown.
Note: *E. nigerrima* McAtee was misidentified by Beamer (1946); see *E. atra* Johnson.

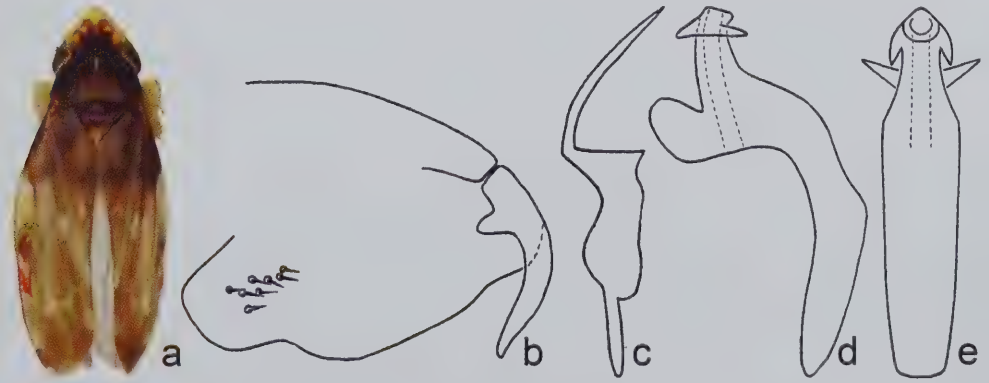
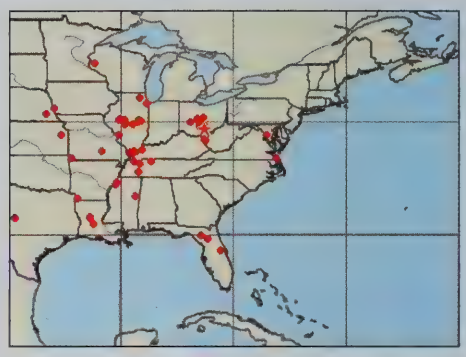


Figure 59. *E. nigerrima* McAtee. c – from Johnson 1935.

60. ***Erasmoneura atra*** (Johnson, 1935), **sp. revalid., new comb.** (Fig. 60)

Erythroneura atra Johnson, 1935:96

Erythroneura nigerrima Beamer, 1946:18 not McAtee 1920, misid.



Description: Length 2.6–2.9 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; pygofer dorsal appendages simple, not extended beyond pygofer apex, slightly curved upward in lateral view. Second point of style apex very short, toothlike; third point of style apex elongate, about as long or longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft curved ventrally, slender in lateral view, round in crossection, with long dorsal distal lobe; ventral processes absent; distal processes long, subapical. Coloration similar to *E. nigra* Gillette.

Type locality: Holotype ♂, USA, Ohio, Hocking Co., Conkles Hollow, Hocking State Forest, 15 IV 1934 (Caldwell), (OSU).

Distribution: Central and eastern USA.

Host plants: Unknown.

Note: *E. atra* Johnson was mistakenly synonymised with *E. nigerrima* McAtee by Beamer (1946).

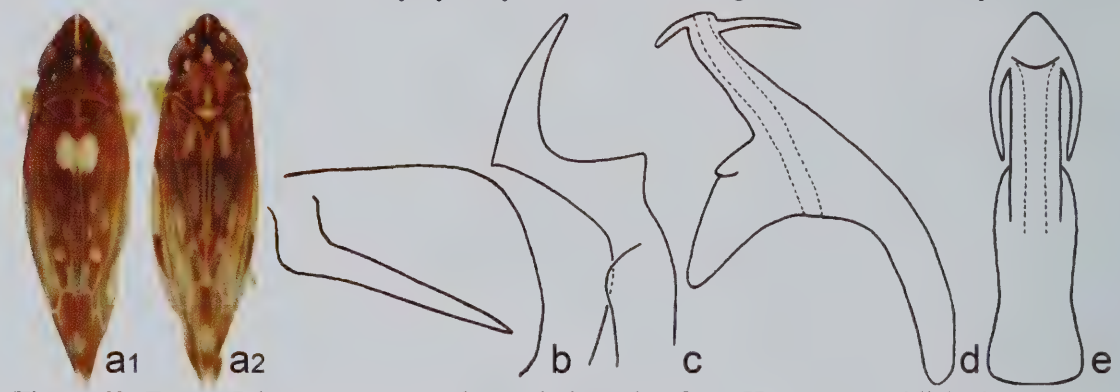
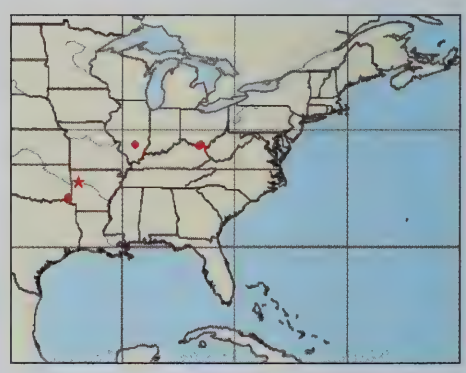


Figure 60. *E. atra* Johnson. a1, a2 – color variations; b – from Hepner, unpublished.

61. ***Erasmoneura caerula*** (Beamer, 1937) (Fig. 61)

Erythroneura caerula Beamer, 1937:10

Erasmoneura caerula Dietrich & Dmitriev, 2006:140

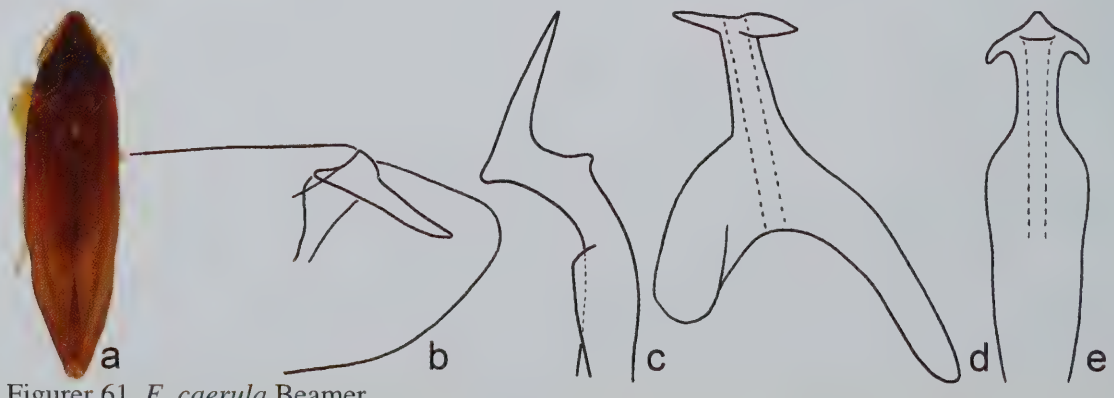


Description: Length 3.1–3.4 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe angulate; pygofer dorsal appendages simple, not extended beyond pygofer apex, straight in lateral view. Second point of style apex very short, tooth like; third point of style apex elongate, longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft straight and slender in lateral view; round in crossection, with long dorsal distal lobe; ventral processes absent; distal processes long, subapical. Dorsum black; anteclypeus pale, concolorous with rest of face; thoracic venter with dark mesosternum, remainder pale.

Type locality: Holotype ♂, USA, Arkansas, Franklin Co., Barnes, 8 VI 1931 (Beamer), (KSEM).

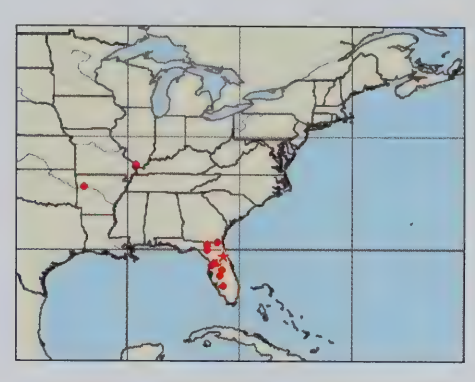
Distribution: Central USA.

Host plants: Unknown.



Figurer 61. *E. caerula* Beamer.

62. ***Erasmoneura rubricata*** (Van Duzee, 1909) (Fig. 62)
Typhlocyba rubricata Van Duzee, 1909:229
Erythroneura rubricata Van Duzee, 1916:77
Erasmoneura rubricata Dietrich & Dmitriev, 2006:140



Description: Length 2.6–3 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; pygofer dorsal appendages simple, not extended beyond pygofer apex, slightly curved upward in lateral view. Second point of style apex very short, tooth like; third point of style apex elongate, about as long as distance between other two points; angle between basal and third points about 90°. Aedeagus with preatrium longer than shaft; shaft straight and broad in lateral view; depressed in crossection, with small dorsal distal lobe, with lateral lobes at base; distal processes long, apical. Uniformly yellow pronotum and forewings, except apices, pink; venter entirely pale.
Type locality: Lectotype ♀, USA, Florida, Putnam Co., Crescent City, Spring 1908, (Van Duzee), (CAS) – here designated.
Distribution: Central and southeastern USA.
Host plants: *Ascyrum hypericoides, Hypericum densiflorum, H. aspalathoides, H. prolificum.*

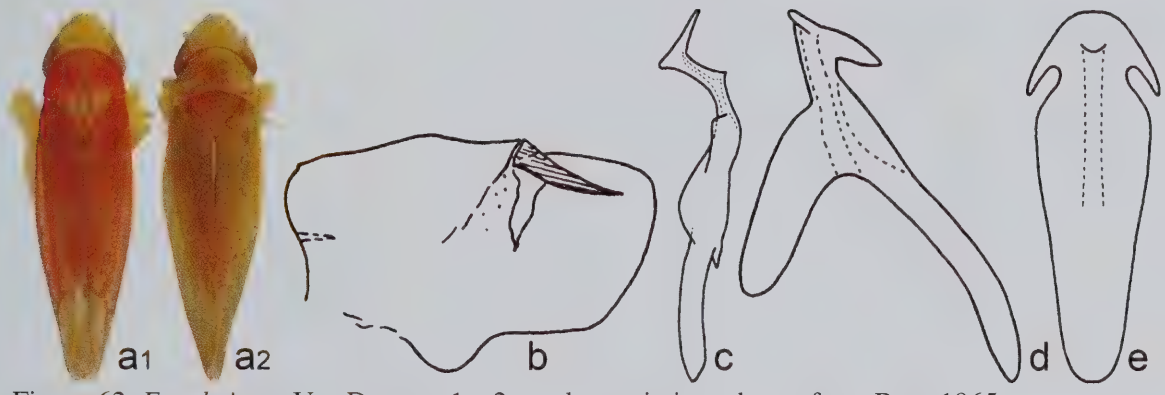
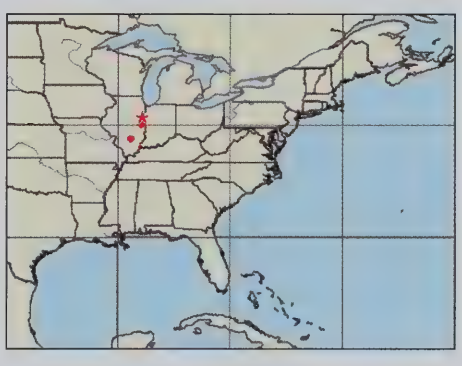


Figure 62. *E. rubricata* Van Duzee. a1, a2 – color variations; b, c – from Ross 1965.

63. ***Erasmoneura margaritae*** Dmitriev & Dietrich **sp.n.** (Fig. 63)



Description: Length 2.7–2.9 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe angulate; dorsal appendages with distinct basal suture, but not movably articulated, simple, not extended beyond pygofer apex, straight or very slightly curved in dorsal view, slightly curved downward in lateral view. Second point of style apex very short, tooth like; third point elongate, about as long as distance between other two points; angle between basal and third points about 90°. Aedeagus with preatrium shorter than shaft; shaft curved ventrally, slender in lateral view, smooth, depressed in crossection, with long dorsal distal lobe, with lateral lobes at base; distal processes long, apical, slender. Dorsum reddish brown; vertex mostly dark, with small pale spots, midline pale or dark; anteclypeus pale, concolorous with rest of face; pronotum almost entirely dark, with three pale specks at anterior margin. Mesonotum almost entirely dark; thoracic venter with dark mesosternum, remainder pale; forewing almost entirely dark, with pale spot at costal margin, and smoked apices.
Diagnosis: *E. margaritae* sp.n. is similar to *E. rubricata* Van Duzee, but the aedeagus shaft is longer and curved dorsally, its dorsal distal lobe is longer, its distal processes are shorter and directed laterad, and the overall coloration is darker.
Type locality: Holotype ♂, USA, Illinois, Iroquois Co., on *Hypericum sp.*, 25 IX 1962 (Ross & Ross), (INHS).

Studied material: Paratypes: 10 ♂, 4 ♀, the same label data (INHS, 1 ♂ MEM). Other studied material from Illinois excluded from paratypes.
Distribution: Illinois.
Host plants: *Hypericum sp.*
Note: The species is named after the first author's wife Margarita Dmitrieva.

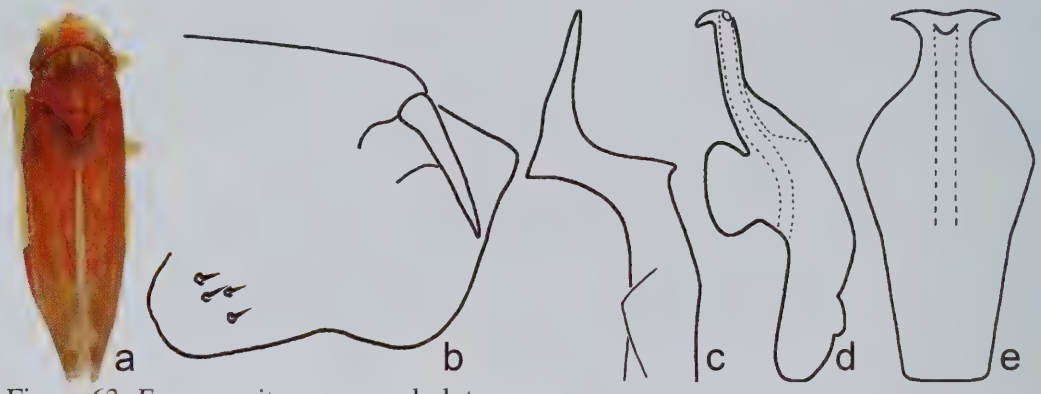
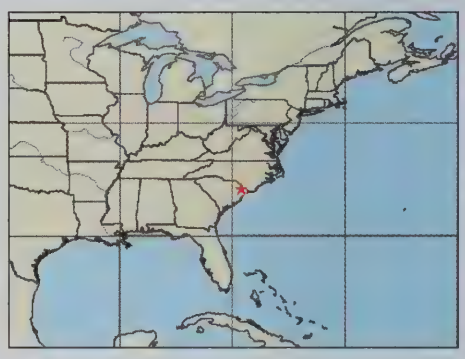


Figure 63. *E. margaritae* sp.n. a – holotype

64. ***Erasmoneura emeljanovi*** Dmitriev & Dietrich **sp.n.** (Fig. 64)



Description: Length 2.6–3 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe angulate; dorsal appendages with distinct basal suture, but not movably articulated, simple, not extended beyond pygofer apex, straight, slightly curved upward in lateral view; ventral appendages absent. Second point of style apex very short, toothlike; third point elongate, longer than distance between other two points; angle between basal and third points less than 90°. Aedeagus with preatrium about as long as shaft; shaft symmetrical, curved dorsally, slender in lateral view, smooth, round in crossection, with long dorsal distal lobe; ventral processes absent; distal processes short, apical, toothlike. Coloration uniformly pale yellow, without pattern.
Diagnosis: *E. emeljanovi* sp.n. is similar to *E. mixta* Beamer, but the aedeagus shaft is curved dorsally, with the distal lobe much longer.
Type locality: Holotype ♂, USA, South Carolina, Marion Co., Mullins, on *Hypericum sp.*, 5 V 1932 (Oman), (KSEM).
Studied material: Paratypes: 9 ♂, 9 ♀, the same label data.
Distribution: Known only from type locality in South Carolina.
Host plants: *Hypericum sp.*
Note: The species is named in honor of Prof. Alexandr F. Emeljanov (Zoological Institute, Russian Academy of Sciences, St. Petersburg), Ph.D. advisor of the first author.

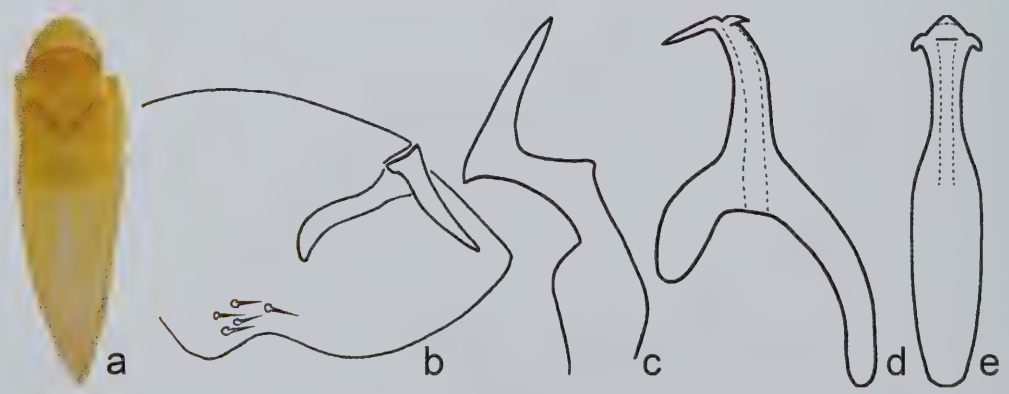
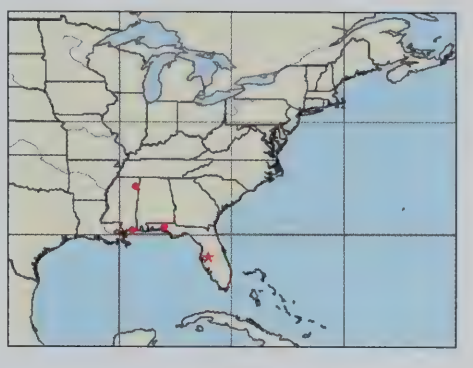


Figure 64. *E. emeljanovi* sp.n. a – holotype.

65. ***Erasmoneura mixta*** (Beamer, 1932) (Fig. 65)
Erythroneura mixta Beamer, 1932i:183
Erasmoneura mixta Dietrich & Dmitriev, 2006:140



Description: Length 2.4–2.7 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages simple, not extended beyond pygofer apex, slightly curved upward in lateral view. Second point of style apex very short, tooth like; third point of style apex elongate, about as long as distance between other two points; angle between basal and third points about 90°. Aedeagus with preatrium about as long as shaft; shaft curved ventrally, slender in lateral view, round in crossection, with long dorsal distal lobe, with lateral lobes at base; distal processes long, apical. Dorsum yellow or pink; anteclypeus pale, concolorous with rest of face or darker; thoracic venter entirely pale or entirely dark.
Type locality: Holotype ♂, USA, Florida, Hillsborough Co., Plant City, on *Hypericum fasciculatum*, 15 VIII 1930 (Beamer), (KSEM).
Distribution: Southeastern USA.
Host plants: *Hypericum fasciculatum, H. aspalathoides*.

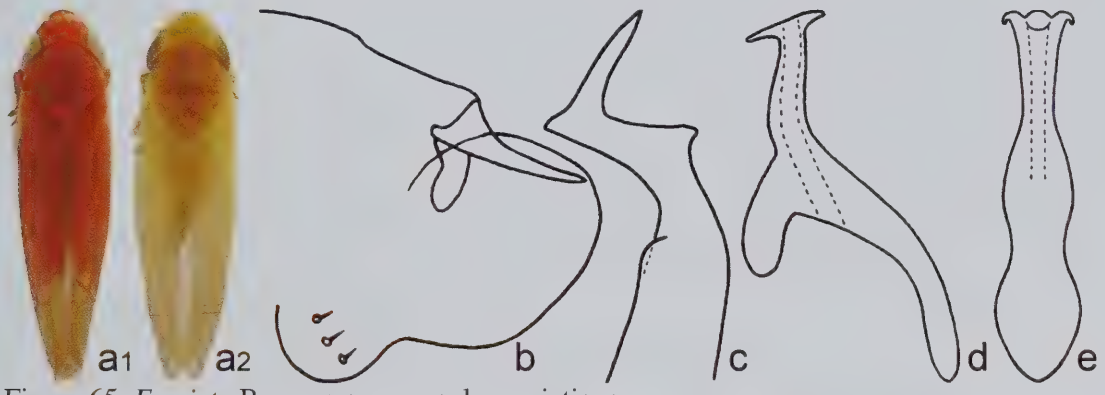
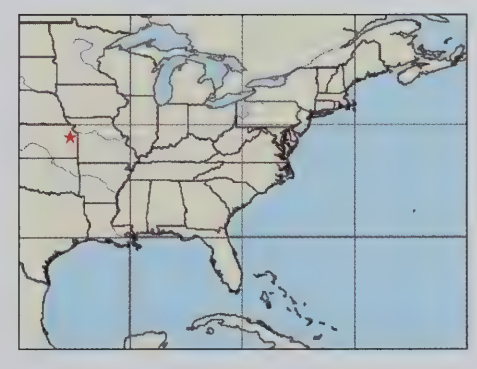


Figure 65. *E. mixta* Beamer. a1, a2 – color variations.

66. ***Erasmoneura bipentagona*** (Beamer, 1927) (Fig. 66)
Erythroneura bipentagona Beamer, 1927:31
Erasmoneura bipentagona Dietrich & Dmitriev, 2006:140



Description: Length 2.7 mm. Dorsum yellow with reddish brown color pattern; vertex unicolorous, pale; anteclypeus pale, concolorous with rest of face; pronotum almost entirely dark; mesonotum pale, with dark lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewings with oblique vittae forming zigzag pattern; clavus largely dark; dark spot at costal margin; apical cell II with distal spot; inner apical cell without brown spot.
Type locality: Holotype ♀, USA, Kansas, Douglas Co., (Beamer), (KSEM).
Distribution: Known only from the type locality in eastern Kansas.
Host plants: Unknown.
Notes: The species is known only from the female holotype. Based on the shape of female sternite VII and color pattern, it may be related to *E. margaritae*.

Figure 66. *E. bipentagona* Beamer.

Genus ***Rossmoneura*** Dietrich & Dmitriev, 2006

Rossmoneura Dietrich & Dmitriev, 2006:148 (Type: *Erythroneura tecta* McAtee, 1920)

Description: Length 2.5–3.6 mm, moderately broad. Head narrower than pronotum; crown fore-margin weakly produced, broadly rounded apically; ocelli absent; face depressed in profile, less than 45° from horizontal. Forewing outer apical cell about 2X as long as wide; second apical cell quadrate (ir crossvein present); third apical cell parallel sided, straight; CuP shorter than segment of CuA between Cu and MP; basal segment of MP shorther than basal segment of CuA; inner apical cell with distinctly angulate base; vannal vein on forewings not visible. Hindwing submarginal vein not extended to wing apex; RA vein present; MP and CuA touching at one point or separated by m-cu crossvein, convergent distally. Front femur AV row with one basal seta distinctly larger than others; PV row without fine basal setae. 2S abdominal apodemes narrow, or broad, extended to posterior margin of sternite III. Pygofer with apex not extended to apex of subgenital plate; lobe rounded; dorsal emargination extended to base of segment; basolateral setae in distinct group, small; with rigid setae on internal surface. Pygofer dorsal appendages not articulated; simple; ventral appendages absent. Sternite IX with median longitudinal internal ridge. Subgenital plates free; lateral margin with angulate subbasal projection; section basad of medial constriction shorter than distal section; with four basal macrosetae uniseriate along margin; with distinct marginal rigid setae forming continuous row. Style preapical lobe prominent; apex with three points; second point long, often longer than third; third point subequal in size or shorter than second; angle between basal and third points about 90°. Aedeagus articulated to connective; dorsal apodeme broadly expanded in lateral view, with distinct V-shaped ligaments connected to pygofer appendages; shaft without dorsal process; with small dorsal distal lobe; with unpaired short ventral process placed basally or near midlength of shaft, close to shaft. Connective median anterior lobe absent; arms long; stem well developed, depressed. Anal tube without processes. Dorsum yellow or white, with reddish brown color pattern; vertex usually with pair of dark preapical spots.

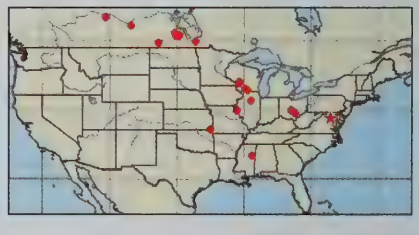
Distribution: Central and eastern USA, southern Canada.

Host plants: Herbs.

Key to Species of the Genus *Rossmoneura*

1. Pygofer dorsal appendage straight in lateral view (Fig. 67b). ..... 67. **R. carbonata** McAtee
1'. Pygofer dorsal appendage curved upward in lateral view (Figs. 68b, 69b). 2
2(1). Pygofer dorsal appendage only slightly curved in lateral view (Fig. 68b). ..... 68. **R. tecta** McAtee
2'. Pygofer dorsal appendages hook-shaped in lateral view (Fig. 69b). ..... 69. **R. calva** Beamer

67. ***Rossmoneura carbonata*** (McAtee, 1920) (Fig. 67, Plate 1g)



Erythroneura tecta var. *carbonata* McAtee, 1920:289

Erythroneura carbonata Beamer, 1946:22

Rossmoneura carbonata Dietrich & Dmitriev, 2006:149

Description: Length 2.5–3 mm. 2S abdominal apodemes large, broad, reach 3S posterior margin. Pygofer lobe rounded; dorsal appendages extended beyond pygofer apex, straight in lateral view. Second point of style apex longer than third; third point very short. Aedeagus with preatrium about as long as shaft; shaft straight and broad in lateral view; round in crossection, with small dorsal distal lobe; with ventral upnaired process arising near midlength of shaft; distal processes absent. Dorsum yellow or white, with brownish or reddish brown color pattern; vertex with pair of black preapical spots; anteclypeus brown or black. Pronotum mostly dark; mesonotum pale, with black lateral triangles; thoracic venter with dark mesosternum, remainder pale. Forewing mostly dark, with several pale specks, large spots at base and apex of clavus, and at costal margin.

Type locality: Holotype ♂, USA, Maryland, Montgomery Co., Plummers Island, 14 XII 1913 (McAtee), (KSEM).
Distribution: Central and eastern USA, southern Canada.
Host plants: *Steironema ciliatum, Glaux maritima, Lysimachia lanceolata.*

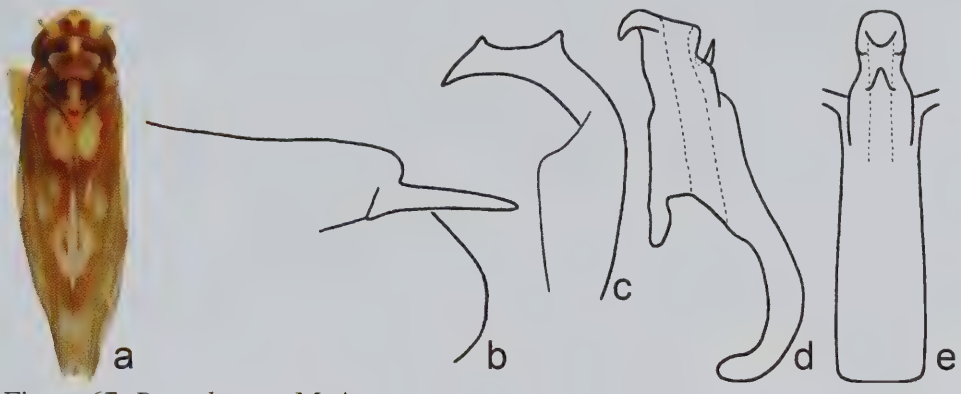
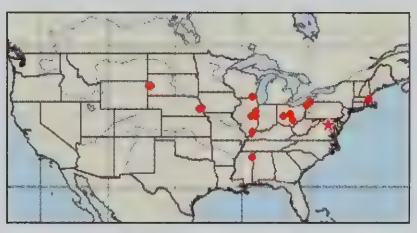


Figure 67. *R. carbonata* McAtee.

68. ***Rossmoneura tecta*** (McAtee, 1920) (Fig. 68)
Erythroneura tecta McAtee, 1920:288
Erythroneura sexpunctata Malloch, 1921:25
Rossmoneura tecta Dietrich & Dmitriev, 2006:149



Description: Length 3.1–3.6 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages extended beyond pygofer apex, slightly curved upward in lateral view. Second point of style apex longer than third; third point very short. Aedeagus with preatrium about as long as shaft; shaft curved ventrally, broad in lateral view; round in crossection, with small dorsal distal lobe, ventral process unpaired, placed basally, close to shaft, shorter than shaft; distal processes short, apical. Dorsum yellow or white, with reddish or brownish color pattern; vertex with pair of black preapical spots; anteclypeus dark. Pronotum dark with pale lateral margins or pale with two longitudinal strips; mesonotum pale, with black lateral triangles; thoracic venter with dark mesosternum, remainder pale; forewing usually with oblique vittae forming zigzag pattern; clavus with separate basal and distal vittae.
Type locality: Holotype ♀, USA, Maryland, Montgomery Co., Plummers Island, among mullen leaves, 25 I 1914 (McAtee), (USNM).
Distribution: Central and eastern USA.
Host plants: ? *Verbascum* sp.

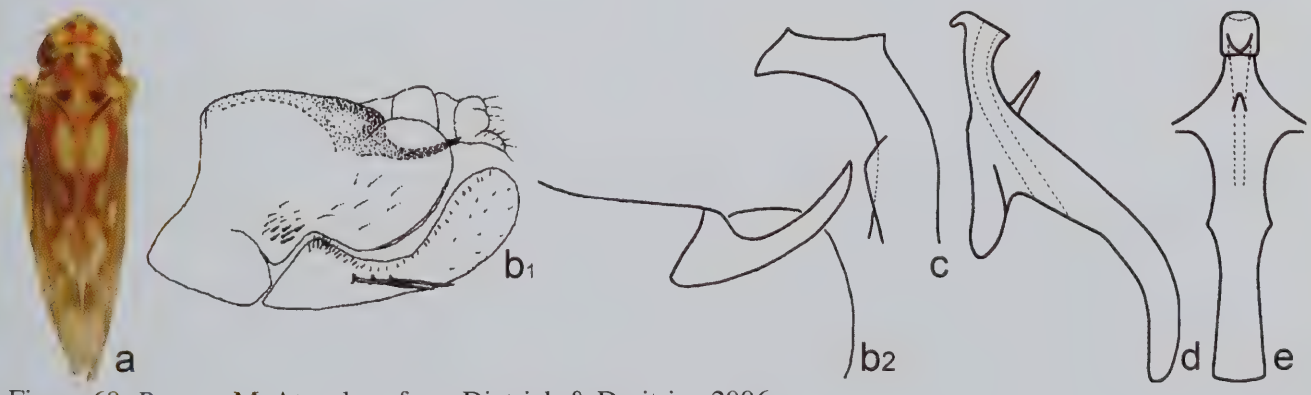
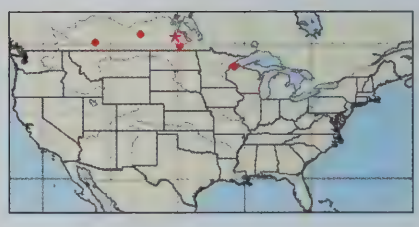


Figure 68. *R. tecta* McAtee. b1 – from Dietrich & Dmitriev 2006.

69. ***Rossmoneura calva*** (Beamer, 1946) (Fig. 69)
Erythroneura calva Beamer, 1946:22
Rossmoneura calva Dietrich & Dmitriev, 2006:149



Description: Length 3–3.6 mm. 2S abdominal apodemes small, narrow, extended dorsomesad. Pygofer lobe rounded; dorsal appendages not extended beyond pygofer apex, strongly curved upward in lateral view. Second point of style apex well developed; third point subequal in size to second. Aedeagus with preatrium about as long as shaft; shaft curved ventrally, broad in lateral view; round in crossection, with small dorsal distal lobe; ventral process unpaired, arising near midlength of shaft; distal processes short, apical. Coloration similar to *R. carbonata* McAtee but paler and without dark spots on crown.
Type locality: Holotype ♂, Canada, Manitoba, Keld, 8 VIII 1937 (Beamer), (KSEM).
Distribution: North-central USA, southern Canada.
Host plants: Unknown.

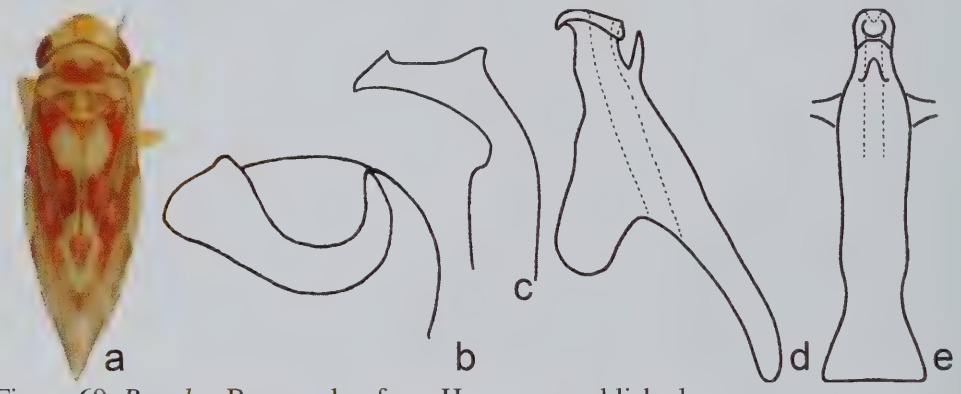


Figure 69. *R. calva* Beamer. b – from Hepner, unpublished.

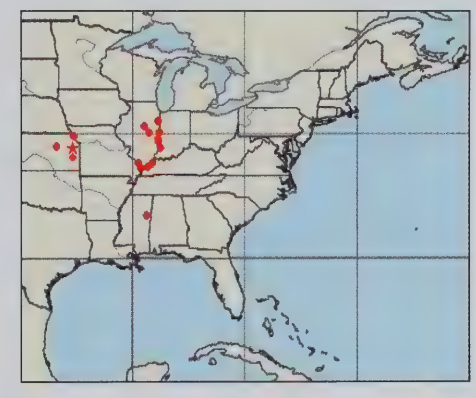
Genus **Hymetta** McAtee, 1919
Hymetta McAtee, 1919:121 (Type: *Tettigonia trifasciata* Say, 1825)
Description: Length 3–3.7 mm, moderately broad. Head narrower than pronotum; crown fore-margin strongly produced and angulate medially; ocelli absent; face depressed in profile, less than 45° from horizontal. Forewing outer apical cell about 2X as long as wide; second apical cell quadrate (ir crossvein present); third apical cell widened distally, straight; CuP longer than segment of CuA between Cu and MP; basal segment of MP shorther than basal segment of CuA; inner apical cell with distinctly angulate base; Pcu not visible. Hindwing submarginal vein not extended to wing apex; RA present; MP and CuA touching at one point or separated by m-cu crossvein, convergent distally. Front femur AV row with one basal seta distinctly larger than others; PV row without fine basal setae. 2S abdominal apodemes large, broad, extended to posterior margin of sternite III. Pygofer apex not extended to apex of subgenital plate; lobe rounded; dorsal emargination extended to base of segment; basolateral setae in distinct group, small; apex with rigid setae on internal surface. Pygofer dorsal appendage with distinct basal suture, but not movably articulated, simple, not extended beyond pygofer apex, straight or very slightly curved in dorsal view, straight in lateral view; ventral appendage absent. Sternite IX without median longitudinal internal ridge. Subgenital plates free; lateral margin with angulate subbasal projection; section basad of medial constriction shorter than distal section; with four basal macrosetae, uniseriate, along margin; with distinct marginal rigid setae forming continuous row. Style preapical lobe prominent; apex truncate and expanded; third point absent. Aedeagus articulated to connective; dorsal apodeme broadly expanded in lateral view, triangular, without distinct connection to anal tube or pygofer appendages; preatrium about as long as shaft; shaft symmetrical, curved dorsally, broad in lateral view, without dorsal process, with basal processes, with or without distal processes. Connective median anterior lobe absent; arms long; stem well developed, depressed. Anal tube without processes. Dorsum yellow or white, with reddish or brown color pattern; vertex, pronotum, and mesonotum pale, apex of scutellum black; forewing with characteristic numerous irregular red or

brownish dots, with or without brown crossband; without dark spot at costal margin; apical cell II without distal spot; inner apical cell without brown spot.
Distribution: USA.
Host plants: Three species recorded from *Vitis* spp., host plants for other two species unknown.

Key to Species of the Genus *Hymetta*

1. Aedeagus with one pair of ventral processes; processes well separated from shaft (Fig. 71d). 2
1'. Aedeagus with two pairs of ventral processes; processes placed close to shaft (Figs. 73d, 74d). 4
2(1). Aedeagus with distal processes (Figs. 71d, 71e). 3
2'. Aedeagus without distal processes (Figs. 70d, 70e). ..... 70. **H. kansasensis** Fairbairn
3(2). Aedeagus ventral processes evenly curved in lateral view; distal processes broad in lateral view (Fig. 71d). ..... 71. **H. balteata** McAtee
3'. Aedeagus ventral processes S-curved in lateral view; distal processes narrow in lateral view (Fig. 72d). ..... 72. **H. anthisma** McAtee
4(1). Aedeagus ventral processes narrow, shorter than shaft; shaft curved dorsad in lateral view (Fig. 73d). ..... 73. **H. trifasciata** Say
4'. Aedeagus ventral processes as long or longer than shaft; one pair much broader than another; shaft straight in lateral view (Fig. 74d). ..... 74. **H. arizoniana** Fairbairn

70. **Hymetta kansasensis** Fairbairn, 1928 (Fig. 70)
Hymetta kansasensis Fairbairn, 1928b:90
Description: Length 3.2–3.5 mm. Aedeagus depressed in crossection; apex truncate in ventral view; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus; distal processes absent. Coloration as described for genus.
Type locality: Holotype ♀, USA, Kansas, Douglas Co., 1925 (Lawson), (KSEM).
Distribution: Central and southeastern USA.
Host plants: *Vitis* spp.



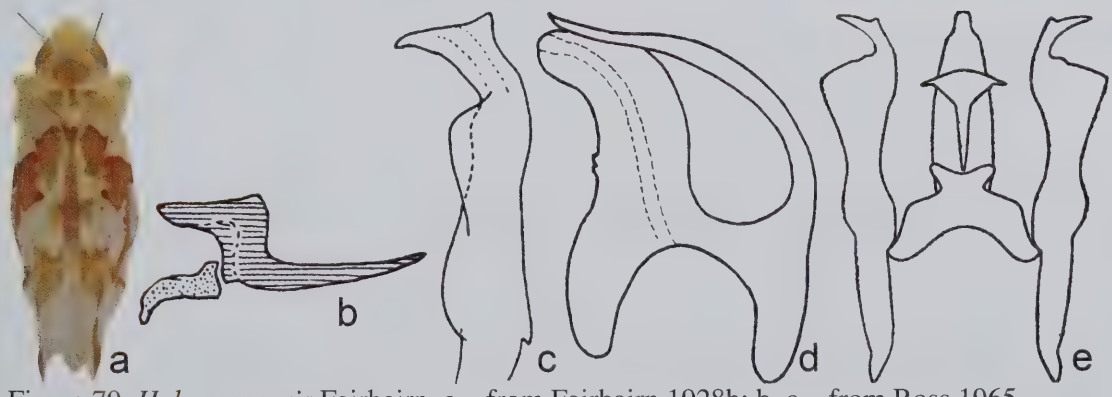
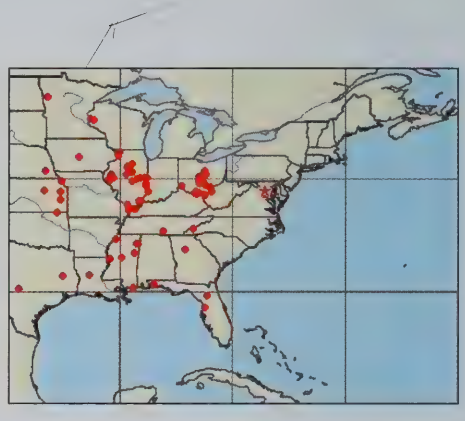


Figure 70. *H. kansasensis* Fairbairn. e – from Fairbairn 1928b; b, c – from Ross 1965.



71. ***Hymetta balteata*** McAtee, 1919 (Fig. 71, Plate 1h)
Hymetta trifasciata var. *balteata* McAtee, 1919:123
Hymetta trifasciata var. *albata* McAtee, 1919:123, **syn.n.**
Hymetta balteata Fairbairn, 1928b:88
Hymetta balteata var. *mediana* Fairbairn, 1928b:89, **syn.n.**

Description: Length 3.1–3.4 mm. Aedeagus compressed in crossection; apex truncate in ventral view; ventral processes placed basally, well separated from shaft, shorter than shaft, parallel to each other on ventral side of aedeagus; distal processes apical, flattened, triangular. Coloration variable, either as described for genus or paler overall.

Type locality: Holotype ♀, USA, Maryland, Montgomery Co., Plummers Island, 14 XII 1913 (McAtee), (USNM).

Distribution: Central and eastern USA.

Host plants: *Vitis* spp.

Note: In the original description (McAtee 1919) recorded the collection date of the holotype incorrectly as 4 XII 1913.

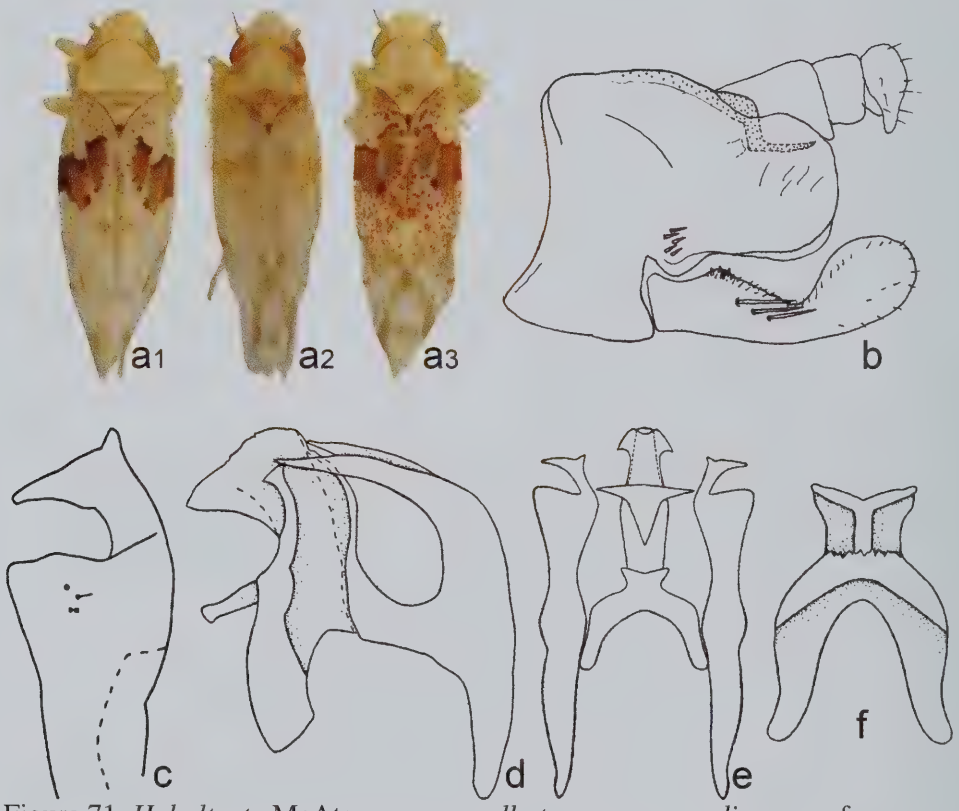
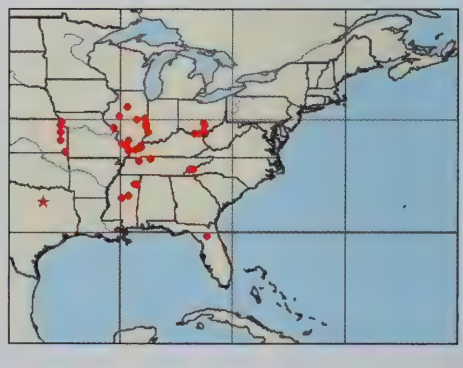


Figure 71. *H. balteata* McAtee. a2 – var. *albata*; a3 – var. *mediana*. e – from Fairbairn 1928b; c, d, f – from Young 1952; b – from Dietrich & Dmitriev 2006.



72. ***Hymetta anthisma*** McAtee, 1919 (Fig. 72)
Hymetta trifasciata var. *anthisma* McAtee, 1919:123
Hymetta distincta Fairbairn, 1928b:87, **syn.n.**
Hymetta balteata var. *anthisma* Fairbairn, 1928b:89
Hymetta anthisma Osborn, 1928b:352

Description: Length 3.3–3.6 mm. Aedeagus round in crossection; apex truncate in ventral view; ventral processes placed basally, well separated from shaft, longer than shaft, parallel to each other on ventral side of aedeagus, sinuate in lateral view; distal processes subapical, slightly flattened.

Coloration typical for genus, wings usually densely covered with red dots.
Type locality: Holotype ♀, USA, Texas, Dallas, on *Vitis sp.*, 12 IX 1907, (USNM).
Distribution: Central and eastern USA.
Host plants: *Vitis* spp.
Note: Fairbairn (1928b) mistakenly listed *H. anthisma* McAtee as a variety of *H. balteata* McAtee. Young (1952) listed the former as a separate species.

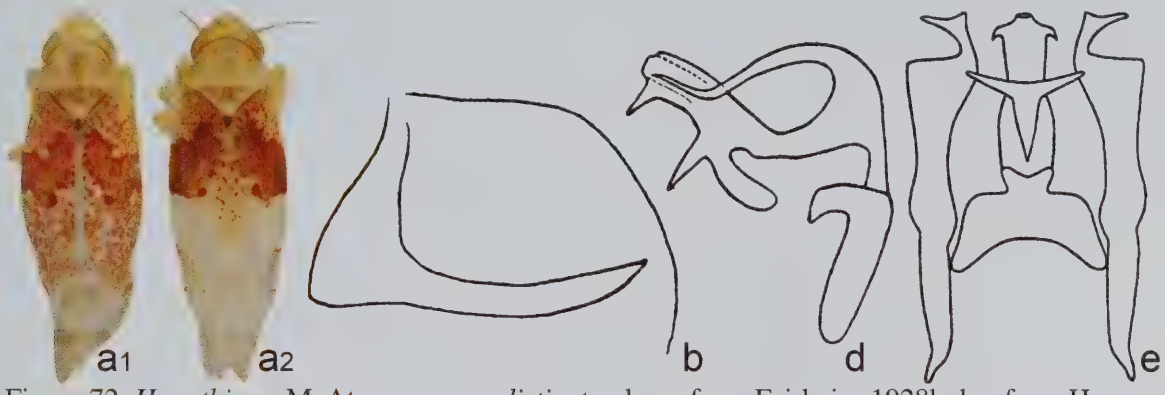
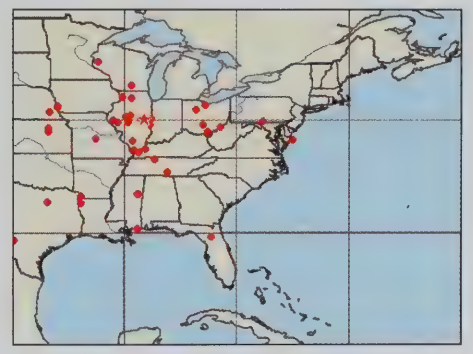


Figure 72. *H. anthisma* McAtee. a2 – var. *distincta*; d, e – from Fairbairn 1928b; b – from Hepner unpublished.

73. ***Hymetta trifasciata*** (Say, 1825) (Fig. 73)
Tettigonia trifasciata Say, 1825:343
Typhlocyba trifasciata Woodworth, 1889:213
Typhlocyba trifascaita Osborn, 1900:12, missp.
Erythroneura trifasciata Van Duzee, 1916:77
Hymetta trifasciata McAtee, 1919:121



Description: Length 3–3.4 mm. Aedeagus compressed in crossection; apex acuminate in ventral view; two pairs of ventral processes placed basally, close to shaft, short; distal processes absent. Coloration as described for genus.
Type locality: Neotype ♂, USA, Illinois, Urbana, on *Cercis canadensis*, 19 IX 1934, (INHS) – here designated.
Distribution: Central and eastern USA.
Host plants: *Vitis spp.*
Note: Because Say's holotype is lost, we designate a neotype to stabilize the concept of this species, the type of the genus. This concept equals that of previous revisers (Fairbairn 1928b, Young 1952).

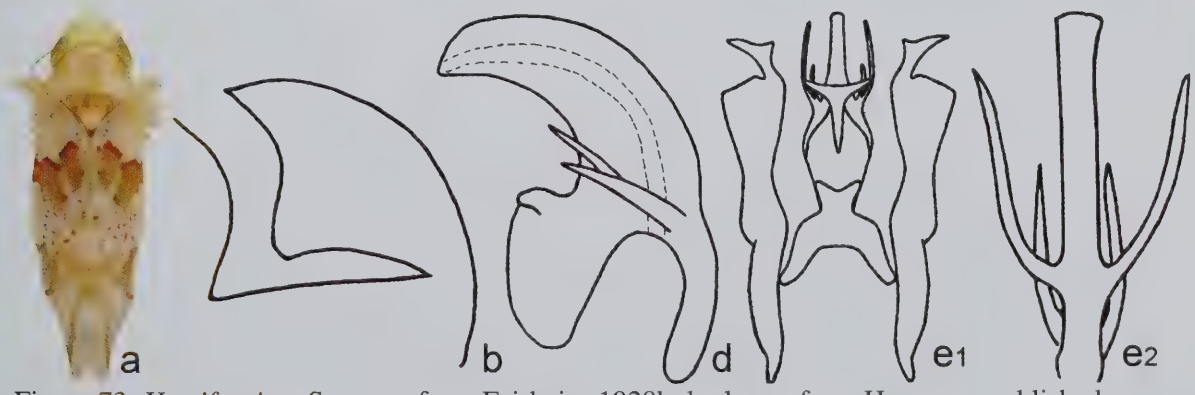
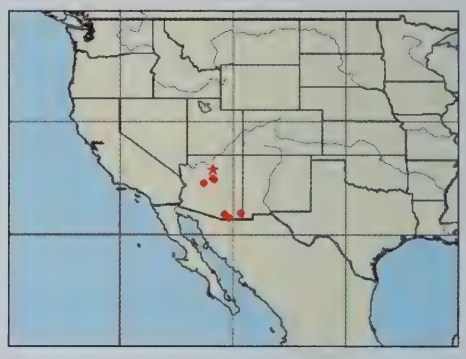


Figure 73. *H. trifasciata* Say. e1 – from Fairbairn 1928b; b, d, e2 – from Hepner unpublished.

74. **Hymetta arizoniana** Fairbairn, 1928 (Fig. 74)
Hymetta arizoniana Fairbairn, 1928b:90



Description: Length 3.3–3.7 mm. Aedeagus round in cross-section; apex truncate in ventral view; two pairs of aedeagus ventral processes placed basally, close to shaft, placed basally; one pair of processes longer than shaft flattened, another pair not flattened, little shorter than shaft; distal processes absent. Coloration typical for genus.
Type locality: Holotype ♂, USA, Arizona, Coconino Co., 13 VIII 1927 (Beamer), (KSEM).
Distribution: Arizona.
Host plants: Unknown.

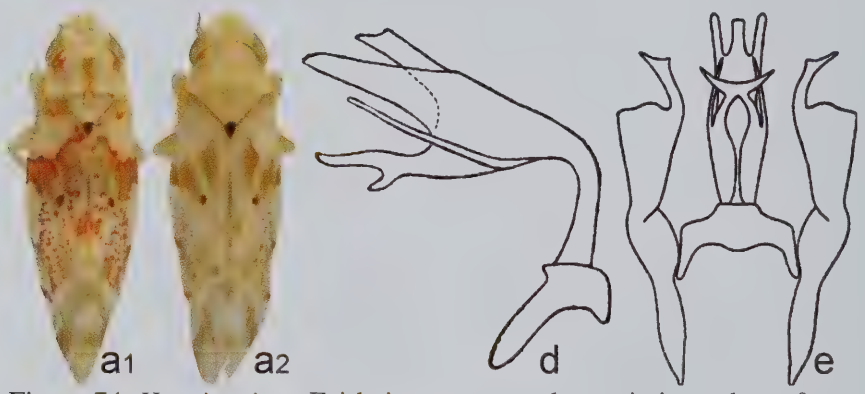


Figure 74. *H. arizoniana* Fairbairn. a1, a2 – color variations. d, e – from Fairbairn 1928b.

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Illinois Natural History Survey
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1816 South Oak Street
Champaign, Illinois 61820
217-333-6880

A Division of the Illinois Department of Natural Resources

ISBN 978-1-882932-14-6

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Illinois Natural History Survey Bulletin
Volume 38, Article 3
April 2008

Illinois Natural History Survey, David L. Thomas, Chief
A Division of the Illinois Department of Natural Resources

Illinois Natural History Survey
Distribution Office
I-Building
1816 South Oak Street
Champaign, IL 61820

Citation:
Dietrich, C.H., and D.A. Dmitriev. 2008. Review of the New World Erythroneurini (Hemiptera: Cicadellidae: Typhlocybinae). II. Genus *Zyginama*. Illinois Natural History Survey Bulletin 38(3):129–176.

Editor: Charles Warwick

US ISSN 0073-4918

US ISBN 1-882932-16-1

Printed by authority of the State of Illinois

P0172233—.75M—04-08

Printed with soy ink on recycled and recyclable paper.

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Acknowledegments

For lending specimens, we are grateful to K.G.A. Hamilton (CNC), C. Freeman (OSU), Z. Falin (KU), E. Riley (TAMU), and S. McKamey (USNM). We also thank G. Moya-Raygoza, H. Brailovsky, and R. Mariño for facilitating field work in Mexico, and T. Erwin and W. Steiner for access to the Smithsonian Amazonian canopy fogging samples. The manuscript was substantially improved based on the comments of two anonymous referees on an earlier version. This work was funded in part by NSF grants DEB-0315373 and DEB-0529679.

Review of the Species of New World Erythroneurini (Hemiptera: Cicadellidae: Typhlocybinae) II. Genus *Zyginama*

Abstract

The 35 previously described species (including 4 junior synonyms) of the New World erythroneurine leafhopper genus *Zyginama* are reviewed and descriptions are provided for 43 new species, 2 from U.S.A., 26 from Mexico, 1 from Panama, and 14 from the Amazon region of South America. The following new synonyms are recognized: *Z. aucta* (McAtee) equals *Erythroneura bilocularis* Van Duzee, syn. n., and *E. inclita* Beamer, syn. n.; *Z. nicholi* (Beamer) equals *E. canyonensis* Beamer, syn. n., and *E. ales* Beamer, syn. n. Separate keys are provided for identification of males from North and South America, all known species are illustrated, and data on their distributions are summarized. Phylogenetic analysis of 40 morphological characters of the 71 species for which males are known yielded a reasonably well resolved estimate of relationships among the included species, but branch support was low overall.

Key words: Auchenorrhyncha, distribution, Homoptera, identification, morphology, phylogeny, taxonomy.

Introduction

The genus *Zyginama* was recently established (Dietrich and Dmitriev 2006) to receive most species of the "*Zygina ritana* species group" recognized by Young (1952). Species in this genus differ from other New World Erythroneurini in having the male pygofer with both dorsal and ventral appendages and a group of enlarged setae ventrolaterally near the base, the anal tube (abdominal segment X) lacking distinct spines, and the aedeagus without a large, unpaired dorsal subbasal process. Species of the genus are very poorly known. Most are recorded from a single locality and host-plant records are lacking for all but a few species. This first attempt to review the genus based on the sparse material available in collections accentuates the need for further collecting and phylogenetic study of the group. The 35 previously recognized species of *Zyginama* are recorded primarily from the southwestern U.S.A. Forty-three additional species, described below, extend the known range of the genus south through Mexico and Central America to Ecuador, Peru, and Brazil. Further collecting in the Neotropical region will undoubtedly lead to the discovery of many additional species of *Zyginama*. The morphology-based phylogenetic analysis of Dietrich and Dmitriev (2006) recovered the included representatives of *Zyginama* as a monophyletic group within a larger clade comprising the mostly North American genera *Aztegina*, *Mexigina*, *Hepzygina*, and *Neozygina*, but that analysis included only three species of *Zyginama*.

Available host records for species recorded from the southwestern U.S.A. indicate that North American species of *Zyginama* occur on trees and shrubs, particularly *Quercus* spp., but no ecological data are available for the majority of species.

This paper synthesizes available morphological, distributional, and host plant data for the known species of *Zyginama*; and provides an estimate of phylogenetic relationships among species, an illustrated key for species identification, and descriptions of new species.

Methods

Morphological terminology follows Dietrich and Dmitriev (2006). Specimens examined, including primary types of all previously described species, are housed in the following collections: California Academy of Sciences, San Francisco (CAS); Canadian National Collection, Ottawa (CNC); Illinois Natural History Survey, Champaign (INHS); U.S. National Museum of Natural History, Washington (USNM); Ohio State University, Columbus (OSU); University of Kansas, Lawrence (KU); Texas A&M University, College Station (TAMU). Verbal species descriptions are provided only for new species; morphological data for previously described species are summarized in a data matrix (Appendix B). In the "Notes" section for previously described species, the average length of males and females examined is given because many original descriptions did not include measurements. Because most species are known only from the type locality, and only a handful of species are recorded from more than three locations, distribution maps are not provided.

Habitus photographs were taken using a Microptics digital micrography system. For each species the best available specimen was photographed. Unfortunately, for many species only the holotype was available and several of these type specimens were in poor condition. To prepare drawings of genitalia, dissected structures were first immersed in glycerine in a well slide and photographed using a Q-Imaging Micropublisher digital camera attached to an Olympus SZX-12 dissecting microscope; the photographs were then enlarged and traced to produce line drawings. For several species, the only available male specimens had the genitalia permanently mounted on slides (Beamer and Knull collections in KU and OSU, respectively). Because pressure from the cover slip tends to distort the structures to various degrees, in the illustrations of these species, the pygofer appendages are extended away from the pygofer margins to a greater degree than they would appear in unmounted specimens. Also, for these species (noted below), it was not possible to illustrate the aedeagus in posterior view.

Many species of New World Erythroneurini are known to exhibit considerable color polymorphism (Dietrich and Dmitriev 2007, Dmitrev and Dietrich 2007). Unfortunately, the degree of intraspecific color polymorphism was impossible to assess for most *Zyginama* species given the paucity of available specimens. Thus, our delimitation of species was based on features of the male genitalia, which we

consider to be more reliable than color pattern. Some taxa previously distinguished based on coloration but lacking distinct differences in the male genitalia (e.g., *Z. nicholi* Beamer and its junior synonyms) are here treated as synonyms. Besides coloration, characters were not found for distinguishing species based on females. Thus, at present, females of many species may only be identified through their association with males.

To assess phylogenetic relationships among species of *Zyginama*, a data matrix comprising coded states for 40 morphological characters (Appendices A and B) was compiled and analyzed under the maximum parsimony criterion using PAUP* 4.0 (Swofford 1998) on a Powermac G5 computer. All characters received equal weight in the analysis, but states of some multistate characters were arranged in hypothetical transformation series and treated as ordered (= additive; see Appendix A). Tree searches were conducted using the heuristic search option with TBR branch swapping of 1000 random taxon addition sequence replicates and a maximum of 500 trees retained in each replicate. Trees were rooted to the outgroup taxon *Mexigina oculata* (McAtee). To measure relative branch support, the Bremer decay index was calculated using the method described by Dietrich and Dmitriev (2006).

Results and Discussion

Phylogenetic Analysis

The analysis of morphological data yielded 1270 equally parsimonious trees of length = 400, consistency index = 0.185, and retention index = 0.528. The Adams consensus of these trees (Fig. 1) was almost completely resolved, but branch support was low, with nearly all consistently resolved branches receiving Bremer support of 1 and no branch receiving support >3. Several clades comprise easily recognizable groups based on features of the male genitalia or color pattern, and recognition of new genera for some of these may eventually be warranted.

Most South American species grouped toward the base of the tree as a paraphyletic grade giving rise to the main North American lineage. Only two species recorded from North America (*Z. ochrescens*, n. sp., and *Z. serrata*, n. sp.) were consistently recovered as sister groups to species endemic to South America. Other clades comprising both North and South American species were not recovered in all most parsimonious trees.

Taxonomy

Typhlocybinae Kirschbaum
Erythroneurini Young
Zyginama Dietrich & Dmitriev
Zyginama Dietrich & Dmitriev, 2006:149
(type species *Erythroneura ritana* Beamer).

Description. Crown moderately to strongly produced medially, with or without pair of indistinct red or brown preapical spots; overall coloration usually pale yellow, variously marked with red or brown, or without distinct markings. Forewing lacking distinct brown or black spots in apical cells; inner apical cell with base oblique. Male pygofer with dorsal appendage well developed, immovably fused to pygofer margin; without macrosetae basad of dorsal appendage (except *Z. intermedia*, n. sp.); ventral appendage present (except *Z. cornigera* (Beamer)), usually elongate; basolateral setal group usually conspicuous, with one or more enlarged setae (reduced or absent in some species). Style apex truncate, footlike, with only two points, preapical lobe well developed. Connective U-shaped, without median anterior lobe, arms short. Aedeagus with dorsal apodeme usually well developed, T-shaped in posterior view, without sclerotized connection to dorsal pygofer appendage or anal tube; shaft usually with paired processes basally, distally, or both; unpaired processes, when present basally, not strongly separated from shaft.

Distribution. Southern USA, south to Brazil and Peru.

Notes. The genus as currently defined is somewhat heterogeneous and recognition of additional genus-group taxa within this assemblage will probably become warranted once the fauna is better known. In particular, several new species from the Amazonian region of Peru and Brazil, although sharing key features with North American *Zyginama*, are similar to various endemic South American erythroneurine genera in coloration and the shape of the head, and, therefore, are only tentatively included in *Zyginama* (see discussion below).

Because there is no apparent overlap in the species composition of North and South America, separate keys are provided for males from these two continents.

Key to Males of North American Species of *Zyginama*

(excluding *Z. dentata* (Gillette) [Fig. 2C] and *Z. ternaria* (Van Duzee) [Fig. 3EE], known only from females)

1 Aedeagus with one or more long spinelike processes arising near base of shaft (Figs. 5b, 7b) rarely arising at or slightly beyond midlength, Fig. 34c), extended distad; distal processes may also be present 2
1' Aedeagus without long spinelike processes, or if such processes present, arising distinctly distad of shaft midlength and extended laterad or basad (Figs. 44c, 48c) 35

2(1) Aedeagus without paired distal processes (angulate flanges or small teeth may be present) (Figs. 5c, 17c) 3
2' Aedeagus with one or more pairs of conspicuous distal processes (Figs. 9b, 10b) 17

3(2) Aedeagus with unpaired basal process closely appressed to shaft, shaft slender, tapered in lateral view, with posterior surface troughlike (Figs. 5b, c) 4
3' Aedeagus with basal processes paired, shaft broad or, if slender, not troughlike posteriorly (Figs. 7b, c) 5

4(3) Length of male <2.7mm, dorsum with conspicuous red markings (Fig. 2A); apex of aedeagus in posterior view distinctly emarginate (Fig. 5c) ..... 1. *Z. aucta* (McAtee)
4' Length of male >2.7mm, dorsum red markings inconspicuous or absent (Fig. 2B); apex of aedeagus in posterior view rounded with weak medial notch (Fig. 6c)..... 2. *Z. merita* (Beamer)

5(3) Aedeagal shaft in lateral view with apex tapered or parallel-sided (Fig. 7b)..... 6
5' Aedeagal shaft in lateral view with apex distinctly expanded (Fig. 19b) 15

6(5) Aedeagal shaft in posterior view parallel-sided or evenly tapered towards apex, without lateral teeth or flanges (Fig. 7b) 7
6' Aedeagal shaft in posterior view with angulate lateral tooth or flange preapically (Fig. 17c) ... 14

7(6) Pygofer lobe with dorsal margin concave preapically, apex not including ventral appendage acute (Fig. 7a) 8
7' Pygofer lobe with dorsal margin convex preapically, apex not including ventral appendage broadly rounded 9

8(7) Body length >3mm; aedeagus with dorsal apodeme in lateral view slender, parallel-sided; basal processes extended nearly to apex of shaft (Fig. 7b).....4. *Z. grandis* (Beamer)
8' Body length <3mm; aedeagus with dorsal apodeme in lateral view strongly broadened dorsally; basal processes not extended beyond midlength of shaft (Fig. 8b) ..... 5. *Z. spectabilis* (Knull & Auten)

9(7) Aedeagus with shaft in lateral view broadest near midlength, crescent-shaped (Figs. 11b, 12b) 10
9' Aedeagus with shaft in lateral view parallel-sided or tapered toward apex (Fig. 14b)..... 11

10(9) Forewing without red markings (Fig. 2K); pygofer with dorsal appendage extended to apex of lobe (Fig. 11a); aedeagus in posterior view with shaft apex acuminate (Fig. 11c) .....9. *Z. munda* (Knull & Auten)
10' Forewing clavus with conspicuous red transcommisural maculae (Fig. 2L); pygofer with dorsal appendage not extended to apex of lobe (Fig. 12a); aedeagus in posterior view with shaft apex broadly rounded ..... 10. *Z. ritana* (Beamer)

11(9) Forewing with conspicuous red markings (Fig. 2M) 12
11' Forewing without conspicuous red markings (Fig. 2P) 13

12(11) Aedeagal shaft in lateral view nearly straight, subequal in length to preatrium; basal processes extended nearly to shaft apex (Fig. 13b); pygofer dorsal appendage tapered, without preapical spine (Fig. 13a)..... 11. *Z. maculipennis*, n. sp.
12' Aedeagal shaft recurved apically, longer than preatrium; basal processes less than half length of shaft (Fig. 14b); pygofer dorsal appendage acuminate, with slender preapical spine (Fig. 14a)... .....12. *Z. cuernavaca*, n. sp.

13(11) Crown without paired spots (Fig. 2O); aedeagal shaft in lateral view with apex evenly rounded, without posterior preapical heel (15b)..... 13. *Z. carapana*, n. sp.
13' Crown with pair of brown preapical spots (Fig. 2P); aedeagal shaft in lateral view footlike, with distinct posterior preapical heel (Fig. 16b)..... 14. *Z. tripunctata* (Beamer)

14(6) Aedeagal shaft in posterior view with pair of small toothlike projections near apex (Fig. 17c), in lateral view with apex slightly curved and blunt (Fig. 17b)..... ..... 15. *Z. coahuilensis*, n. sp.
14' Aedeagal shaft in posterior view with pair of angulate lateral flanges (Fig. 18b), in lateral view with attenuate apical extension bent at nearly right angle to remainder of shaft (Fig. 18c)..... ..... 16. *Z. orizaba*, n. sp.

15(5) Aedeagal shaft in posterior view with pair of angulate lateral flanges (Fig. 19c), in lateral view without angulate projection on dorsal margin (Fig. 19b)..... 17. *Z. rodmani*, n. sp.
15' Aedeagal shaft in posterior view without pair of angulate lateral flanges (Fig. 20b), in lateral view with angulate projection on dorsal margin at or basad of midlength (Fig. 20c)..... 16

16(15) Aedeagal shaft in lateral view with falcate posteroapical projection, dorsal angulate projection near base (Fig. 20b)..... 18. *Z. malleta*, n. sp.
16' Aedeagal shaft in lateral view without falcate posteroapical projection, dorsal angulate projection near midlength (Fig. 21b)..... 19. *Z. zitacuarensis*, n. sp.

17(2) Aedeagal shaft with single spinelike basal process posteriorly (22b, c)..... 18
17' Aedeagal shaft with pair of spinelike basal processes (Fig. 25b, c)..... 20

18(17) Aedeagus with posterior preapical projection (Fig. 23b); pygofer with dorsal appendage not bent abruptly ventrad in distal half (Fig. 23a)..... 19
18' Aedeagus without posterior preapical projection; pygofer with dorsal appendage bent abruptly ventrad in distal half (Fig. 22a).....20. *Z. rubrocta*, n. sp.

19(18) Aedeagus with posterior preapical projection falcate, shaft with auriculate basolateral lobes (Fig. 23b)..... 21. *Z. iguala* (Ross)
19' Aedeagus with posterior preapical projection blunt, shaft without auriculate basolateral lobes (Fig. 24b).....22. *Z. novella* (Knull & Auten)

20(17) Aedeagus in lateral view attenuate apically (Fig. 9b); pygofer with dorsal margin concave preapically, apex (not including ventral appendage) acute (Fig. 9a)..... 21
20' Aedeagus in lateral view with apex truncate or bluntly rounded (Fig. 25b); pygofer with dorsal margin convex preapically, apex (not including ventral appendage) rounded (Fig. 25a)..... 23

21(20) Dorsal color pattern consisting of bold transverse reddish bands, crown pale without distinct markings (Fig. 2F).....6. *Z. nicholi* (Beamer)
21' Dorsal color pattern consisting of large symmetrically arranged reddish spots, crown with paired red or brown spots (Fig. 2J)..... 22

22 Aedeagus with basal processes straight; paired distal processes broad, rounded (Fig. 9b) ..... 7. *Z. rubicunda* (Beamer)
22' Aedeagus with basal processes abruptly bent anterad preapically; paired distal processes slender, acuminate (Fig. 10b) ..... 8. *Z. rossi*, n. sp.

23(20) Aedeagus in lateral view with unpaired acute compressed projection just posteroventrad of gonopore (Fig. 25b) 24
23' Aedeagus in lateral view with area just posteroventrad of gonopore flat or rounded (Fig. 28b).. 25

24(23) Aedeagus with gonopore in lateral view entire, shaft with pair of angulate subbasal projections on dorsal margin (Fig. 25b) ..... 23. *Z. arizonica* (Knull & Auten)
24' Aedeagus with gonopore in lateral view emarginate, shaft without angulate subbasal projections on dorsal margin (Fig. 26b) ..... 24. *Z. elongata*, n. sp.

25(23) Aedeagus with apex in lateral view bent dorsad at 90° angle to remainder of shaft (Fig. 27b) 26
25' Aedeagus with apex in lateral view evenly curved (Fig. 31b) 28

26(23) Aedeagal shaft in lateral view with dorsal and ventral margins strongly arcuate, basal processes strongly divergent from shaft (Fig. 27b) ..... 25. *Z. enigmata*, n. sp.
26' Aedeagal shaft in lateral view with dorsal and ventral margins nearly straight (Fig. 28b) 27

27(26) Aedeagal shaft in lateral view broad basally, abruptly narrowed near midlength, distal processes flattened and angulate subbasally (Fig. 28b) ..... 26. *Z. queretarensis*, n. sp.
27' Aedeagal shaft in lateral view slender throughout length, distal processes slender (Fig. 29b) .... 27. *Z. obscura* (Beamer)

28(25) Aedeagus with paired distal processes lamelliform (Fig. 30c) 29
28' Aedeagus with paired distal processes slender (branched or unbranched) (Fig. 32b) 30

29(28) Distal processes of aedeagus each with three angulate projections (Fig. 30c) .... 28. *Z. angulata*, n. sp.
29' Distal processes of aedeagus with a single projection (Fig. 31b) ..... 29. *Z. durangensis*, n. sp.

30(28) Pygofer dorsal appendage with preapical spine (Fig. 32a) 31
30' Pygofer dorsal appendage without preapical spine (Fig. 34a) 32

31(30) Preapical spine of pygofer dorsal appendage strongly divergent (Fig. 32a) .... 30. *Z. unicolor* (Beamer)
31' Preapical spine of pygofer dorsal appendage not divergent (Fig. 33a) .... 31. *Z. sola* (Knull & Auten)

32(30) Aedeagus with distal processes unbranched, subbasal processes arising near base of shaft (Fig. 36b, c) 34
32' Aedeagus with distal processes branched or, if unbranched, with subbasal processes arising near midlength of shaft (Fig. 34b, c) 33

33(32) Aedeagus with subbasal processes arising near midlength of shaft (Fig. 34b); pygofer without ventral appendage (Fig. 34a) ..... 32. *Z. cornigera* (Beamer)
33' Aedeagus with subbasal processes arising near base (Fig. 35b); pygofer with ventral appendage well developed (Fig. 35a) ..... 33. *Z. erosa* (McAtee)

34(32) Aedeagus in posterior view with distal processes extended ventrolaterad (Fig. 36c) ..... 34. *Z. casta* (Beamer)
34' Aedeagus in posterior view with distal processes extended dorsolaterad (Fig. 37c) ..... 35. *Z. agnata* (Knull & Auten)

35(1) Aedeagus without paired distal processes (Figs. 38b, 39b) 36
35' Aedeagus with paired processes arising at or beyond midlength of shaft (Fig. 44b) 41

36(35) Aedeagal shaft with angulate subbasal dorsal projection (Fig. 39b) 37
36' Aedeagal shaft without angulate subbasal dorsal projection (Fig. 41b) 39

37(36) Aedeagus with unpaired asymmetrical process posteroventrad of gonopore (Figs. 38b, c) ... 36. *Z. panamensis*, n. sp.
37' Aedeagus without unpaired process posteroventrad of gonopore 38

38(37) Aedeagal shaft in lateral view with apex bluntly rounded (Fig. 39b); pygofer dorsal appendage branched (Fig. 39a) ..... 37. *Z. colima*, n. sp.
38' Aedeagal shaft with apex lanceolate (Fig. 40b); pygofer dorsal appendage unbranched (Fig. 40a) ..... 38. *Z. lanceolata*, n. sp.

39(37) Aedeagal shaft in lateral view S-shaped, apex terminating in median posteroventrally directed spine (Fig. 41b) ..... 39. *Z. tricolor* (Beamer)
39' Aedeagal shaft in lateral view recurved, apex without median spine 40

40(39) Aedeagus with gonopore arising near apex of shaft (Fig. 42b); pygofer dorsal appendage straight, strongly divergent from lobe (Fig. 42a) ..... 40. *Z. tolteca*, n. sp.
40' Aedeagus with gonopore arising near base of shaft (Fig. 43b); pygofer dorsal appendage sinuate, weakly divergent from lobe (Fig. 43a) ..... 41. *Z. nuda* (Knull & Auten)

41(35) Aedeagal shaft with more than one pair of lateral projections distad of midlength (Fig. 45b, c) 42
41' Aedeagal shaft with one pair of branched or unbranched lateral projections distad of midlength 48

42(41) Aedeagus in lateral view with shaft distinctly arcuate, with dorsoapical projection forming ca. 90° angle with remainder of shaft (Fig. 45b) 43
42' Aedeagus in lateral view with shaft straight or recurved, dorsoapical projection if present not forming 90° angle with remainder of shaft (Fig. 46b) 44

43(42) Aedeagus in lateral view with unpaired distal process strongly recurved, lateral processes much longer than maximum width of shaft in posterior view (Fig 44b) ..... *Z. brunnedorsum*, n. sp.
43' Aedeagus in lateral view with unpaired distal process straight, lateral processes little if any longer than maximum width of shaft in posterior view (Fig. 45b) ..... 43. *Z. pinalensis*(Beamer)

44(42) Aedeagus without preatrium; shaft with pair of distally branched preapical projections (Fig. 46b) 45
44' Aedeagus with preatrium well developed, more than half length of shaft; shaft without branched preapical projections (Fig. 48b) 46

45(44) Pygofer with dorsal appendage slender, acuminate (Fig. 46a) ..... 44. *Z. triceroprocta* (Beamer)
45' Pygofer with dorsal appendage broad, apex bifid (Fig. 47a) ..... 45. *Z. multifurca*, n. sp.

46(44) Aedeagus with ventrally directed spine ventrad of gonopore (Fig. 48b) ..... 46. *Z. colorada*, n. sp.
46' Aedeagus without ventrally directed spine ventrad of gonopore 47

47(46) Aedeagus in lateral view abruptly bent dorsad at 90° angle near gonopore; paired preapical processes bifid (Fig. 49b) ..... 47. *Z. vittata*, n. sp.
47' Aedeagus in lateral view not abruptly bent, acuminate distally, with pair of slender processes dorsad of gonopore and shorter pair of triangular projections ventrad of gonopore (Fig. 50b) ..... 48. *Z. cimmaroni* (Beamer)

48(41) Pygofer dorsal appendage with angulate preapical projection (Fig. 51a) 49
48' Pygofer dorsal appendage acuminate or blunt, without preapical projection (Figs. 53a, 55a) 50

49(48) Aedeagal shaft in lateral view broad, arcuate, apex with dorsal and ventral spines (Fig. 51b) ..... 49. *Z. inornata* (Beamer)
49' Aedeagal shaft in lateral view slender, nearly straight; apex attenuate, without spines (Fig. 52b) ..... 50. *Z. utahna* (Beamer)

50(48) Pygofer dorsal appendage blunt apically (Fig. 53a) 51
50' Pygofer dorsal appendage acute apically (Fig. 56a) 53

51(50) Pygofer dorsal appendage serrate apically (Fig. 53a); aedeagal shaft in lateral view less than twice as long as its maximum width (Fig. 53b) ..... 51. *Z. serrata*, n. sp.
51' Pygofer dorsal appendage not serrate apically; aedeagal shaft in lateral view more than twice as long as its maximum width 52

52(51) Aedeagus with apex broadly angulate apically, paired processes shorter than shaft width (Fig. 54b) ..... 52. *Z. spatulata*, n. sp.
52' Aedeagus with apex bluntly rounded apically, paired processes longer than shaft width (Fig. 55b) ..... 53. *Z. ochrescens*, n. sp.

53(50) Aedeagus in posterior view with apex bi- or trifurcate (Figs. 56c, 57c), shaft in lateral view with dorsal margin convex (Figs. 56b) 54
53' Aedeagus in posterior view with apex acuminate or rounded (Figs. 58c, 60c), shaft in lateral view concave dorsally (Figs. 58b) 55

54(53) Aedeagus in lateral view with processes curved anterodorsad (Fig. 56b) ..... 54. *Z. toluca*, n. sp.
54' Aedeagus in lateral view with processes extended anterovenrad (Fig. 57b) ..... 55. *Z. pallescens*, n. sp.

55(53) Aedeagus in posterior view with apex rounded, distal processes bifid (Fig. 58c) ..... 56. *Z. blanda* (Knull & Auten)
55' Aedeagus in posterior view with apex acuminate, distal processes acuminate (Fig. 60c) 56

56(55) Aedeagus with processes short, triangular (Fig. 59b); pygofer dorsal appendage straight (Fig. 59a) ..... 57. *Z. pallenta* (Beamer)
56' Aedeagus with processes elongate, slender (Fig. 60b); pygofer dorsal appendage falcate (Fig. 60a) ..... 58. *Z. olmeca*, n. sp.

1. *Zyginama aucta* (McAtee) (Figs. 2A, 5)
Erythroneura obliqua var. *aucta* McAtee, 1920a:279
Erythroneura dentata bilocularis Van Duzee,1924a: 233, **new synonym**
Erythroneura aucta, Beamer, 1932i:123
Erythroneura inclita Beamer, 1934a:44, **new synonym**
Zygina aucta, Young, 1952:75
Zyginama aucta, Dietrich & Dmitriev, 2006:149
Type locality: San Diego Co., California [CAS].
Distribution: USA: California.
Notes: Length of male 2.8 mm, female 3.0 mm. Study of the holotypes of *E. dentata bilocularis* Van Duzee (San Diego Co., California [CAS]) and *E. inclita* Beamer (San Jacinto Mts., California) indicates that both are synonyms of *Z. aucta* (McAtee). McAtee's holotype is a female, but the coloration of this species is distinctive and, thus, the interpretation of *Z. aucta* embodied in Beamer's male "allotype" (KU) appears to be correct. Beamer (1932i) recorded *Quercus douglasi* as the host plant of this species.

2. *Zyginama merita* (Beamer) (Figs. 2B, 6)
Erythroneura merita Beamer, 1932i:127
Zygina merita, Young, 1952:76
Zyginama merita, Dietrich & Dmitriev, 2006:150
Type locality: San Jacinto Mts., California [KU].
Distribution: USA: California.
Notes: Length of male 3.5 mm, female 3.7 mm. Beamer (1932i) recorded this species from "live oak".

3. *Zyginama dentata* (Gillette) (Fig. 2C)
Typhlocyba dentata Gillette, 1898a:765
Erythroneura dentata, Kirkaldy, 1907d:69
Zygina dentata, Young, 1952:75
Zyginama dentata, Dietrich & Dmitriev, 2006:149
Type locality: Folsom, California [USNM].
Distribution: USA: California.
Notes: Length of female 3.7 mm, male unknown. To help fix the identity of the species, one of two female syntypes from Gillette's collection in the USNM (type no. 3453) is here designated lectotype. No male specimens of this species are known. This species is very similar to *Z. aucta* in coloration and in the shape of the seventh abdominal sternite of the female, but differs in being considerably larger.

4. *Zyginama grandis* (Beamer) (Figs. 2D, 7)
Erythroneura grandis Beamer, 1929b: 127
Zygina grandis, Young, 1952:76
Zyginama grandis, Dietrich & Dmitriev, 2006:150
Type locality: Oak Creek Canyon, Arizona [KU].
Distribution: USA: Arizona.
Notes: Length of male 3.5 mm, female, 3.7 mm.

5. *Zyginama spectabilis* (Knull & Auten) (Figs. 2E, 8)
Erythroneura spectabilis Knull & Auten 1938a:533
Zygina spectabilis, Young, 1952:76
Zyginama spectabilis, Dietrich & Dmitriev, 2006:150
Type locality: Huachuca Mts., Arizona [OSU].
Distribution: USA: Arizona.
Notes: Length of male 3.0 mm, female 3.1 mm.

6. *Zyginama nicholi* (Beamer) (Figs. 2F–H, 9)
Erythroneura nicholi Beamer, 1927a:30
Erythroneura canyonensis Beamer, 1929b:120, **new synonym**
Erythroneura ales Beamer, 1932i:124, **new synonym**
Zygina nicholi, Young, 1952:76
Zyginama nicholi, Dietrich & Dmitriev, 2006:150
Type locality: Santa Rita Mts., Arizona (elev. 4,500 ft.) [KU].
Distribution: USA: Arizona, Utah.
Notes: Length of male 2.7 mm, female 3.0 mm. The taxa here treated as junior synonyms appear to represent color forms of a single species. Comparison of the male genitalia of the holotypes of *E. canyonensis* and *E. ales* to those of *E. nicholi* revealed only slight differences in the length of the basal aedeagal processes. These vary among individuals having the same coloration.

7. *Zyginama rubicunda* (Beamer) (Fig. 2I)
Erythroneura rubicunda Beamer, 1929b: 126
Zygina rubicunda, Young, 1952:76
Zyginama rubicunda, Dietrich & Dmitriev, 2006:150

Type locality: Pinal Co., Arizona [KU].
Distribution: USA: Arizona.
Notes: Length of male 2.8 mm, female 3.0 mm. Beamer's holotype of *E. rubicunda* [KU] is a female. Male specimens from the Huachuca Mts., Arizona [OSU] and identified as "*Erythroneura rubicunda*" by Knull closely resemble the female holotype in size and color pattern, and the male pygofer and genitalia are nearly identical to those of *Z. nicholi* (Fig. 9). Nevertheless, *Z. rubicunda* is retained as a valid species based on its distinctive coloration, which more closely resembles that of *Z. grandis* and *Z. rossi*, n. sp.

8. *Zyginama rossi*, n. sp. (Figs. 2J, 10)
Description. Length of male 3.1-3.3, female 3.2-3.3. Ground color pale yellow, heavily marked with reddish orange. Face mostly reddish brown with two pairs of symmetrical pale spots dorsally; crown-face transition pale yellow; crown pale yellow with pair of faint brown spots preapically near midline and pair of small orange maculae more laterad. Pronotum mostly reddish orange; midline, posterior margin, and five anterior spots pale. Mesonotum orange except pale midline; scutellum orange except pale anterolateral corners. Forewing clavus with orange maculae at base, near midlength, and at apex; corium with costal area orange basally and distad of brochosome field; orange maculae also present near midlength and apex of brachial cell and along vein M near midlength; apex infuscated. Venter of thorax and abdomen dark reddish brown. Head narrower than pronotum; crown in dorsal view slightly longer medially than next to eye, anterior margin forming 90° angle. Head (Fig. 2J) subequal to pronotum in width; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 10a) with dorsal appendage arising near base, not elevated above margin of lobe, acuminate, slightly decurved, extended to midlength of lobe; ventral appendage arising preapically, short, curved dorsad; lobe between appendages acute, concave dorsally; ventrolateral setal group with ~9 enlarged setae. Aedeagus (Figs. 10b, c) without preatrium; dorsal apodeme in lateral view slightly broadened dorsally; shaft in lateral view moderately broad, nearly straight, terminating in anterodorsally directed acuminate spine; with preapical pair of slender lateral processes extended ventrad; paired subbasal processes arising posteriorly near base, closely paralleling shaft to near gonopore, with apices abruptly bent anterad; gonopore preapical on posterior surface.
Material examined. Holotype male, USA: Illinois, W. Karnak, 24 September 1952 (Ross and Evers, on *Quercus lyrata*); 1 female paratype, same data; 3 male and 1 female paratypes, USA: Illinois, Grantsburg, 28 August 1952 (Rich. and Stannard, on *Quercus lyrata*); 1 female paratype, same data except 23 September 1953 (Ross and Evers, on *Quercus palustris*) [INHS]; 1 male paratype, USA: Mississippi, Fulton, 15 June 1935 (D.W. Grimes) [OSU].
Notes. This species closely resembles *Z. rubicunda* (cf. Fig. 2I), but differs in having a pair of brown spots on the crown, the distal processes of the aedeagus slender and the basal processes long and abruptly bent preapically. The species is named in memory of the late Prof. H.H. Ross, collector of the holotype and a pioneer in the study of New World Erythroneurini. It is one of only two species of *Zyginama* recorded from east of the Mississippi River (the other being *Z. tripunctata*) and the only one known from the midwestern U.S.A.

9. *Zyginama munda* (Knull & Auten) (Figs. 2K, 11)
Erythroneura munda Knull & Auten 1938a:534
Erythroneura modula Knull & Auten 1938a:535
Zygina munda, Young, 1952:76
Zyginama munda, Dietrich & Dmitriev, 2006:150
Type locality: Chiricahua Mts., Arizona [OSU].
Distribution: USA: Arizona.
Notes: Length of male 3.0 mm, female 3.3 mm.

10. *Zyginama ritana* (Beamer) (Figs. 2L, 12)
Erythroneura ritana Beamer, 1934c:286
Zygina ritana, Young, 1952:76
Zyginama ritana, Dietrich & Dmitriev, 2006: 150
Type locality: Santa Rita Mts., Arizona [KU].
Distribution: USA: Arizona.
Notes: Length of male 3.0 mm, female 3.2 mm. Beamer (1934c) recorded this species from "blue oak." The illustration of the aedeagus of this species provided by Dietrich and Dmitriev (2006) omitted the paired basolateral processes of the aedeagus.

11. *Zyginama maculipennis*, n. sp. (Figs. 2M, 13)

Description. Length of male 3.5 mm. Ground color dull yellow; pronotum orange posteromesad; mesonotum and scutellum orange-brown; forewing with four red maculae, two on clavus and two more distad along vein Cu. Head (Fig. 2M) narrower than pronotum, crown in dorsal view with median length distinctly greater than length next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 13a) with dorsal appendage arising near midlength, not elevated above margin of lobe, short, strongly tapered, curved mesad, not extended to apex of lobe; ventral appendage arising near apex, long, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group absent. Aedeagus (Figs. 13b, c) with preatrium as long as shaft; dorsal apodeme in lateral view broadly rounded; shaft in lateral view short, slender, nearly straight; paired subbasal appendages not divergent from shaft in lateral view, evenly divergent in posterior view; apex beyond gonopore compressed and attenuate; gonopore preapical on posterior surface.

Material examined. Holotype male, MEXICO, Michoacan, Carapan, km 432, 2 October 1941 (DeLong, Good, Caldwell, Plummer) [INHS].

Notes. This species resembles *Z. colima* in coloration but differs in having the pygofer dorsal appendage short and relatively broad, the ventrolateral setal group lacking; and the aedeagus with the preatrium elongate, the shaft very short and slender, and the basal paired processes well developed. The species name, an adjective meaning "spot wing," refers to the spotted forewings.

12. *Zyginama cuernavaca*, n. sp. (Figs. 2N, 14)

Description. Length of male 4.0-4.2 mm, female 4.2 mm. Ground color pale yellow; face mostly brown; crown with small dark brown spot apically; pronotum with pair of small sublateral brown spots and pair of large orange submedial triangles, posterior margin white; mesonotal triangles orange; scutellum apex black; forewing base orange, clavus with orange medial blotch, brachial cell with two orange blotches, vein M bordered with orange near midlength; mesosternum and abdomen except genital plates mostly dark brown. Head (Fig. 2M) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 14a) with dorsal appendage arising near midlength, slender, straight, not elevated above pygofer margin, bifurcate distad of midlength with branches closely appressed to each other, extended slightly beyond apex of lobe; ventral appendage arising near apex, long, extended dorsomesad; lobe between appendages rounded; ventrolateral setal group with ~6 enlarged setae. Aedeagus (Figs. 14b, c) with preatrium short; in lateral view with dorsal apodeme broadened dorsad; shaft slender, irregularly recurved, tapered distally, with pair of short subbasal processes not extended beyond shaft midlength, divergent in posterior view; distal processes absent; apex in posterior view acuminate; gonopore preapical on posterior margin.

Material examined. Holotype male, MEXICO, km 66 Mexico-Cuernavaca Rd., 17 August 1936 (Ball and Stone); 3 male and 2 female paratypes, same data [OSU].

Notes. This species closely resembles *Z. tripunctata* in coloration but differs in having the dorsal pygofer appendage more elongate and divided distally into two parallel spines. The species name, an adjective, refers to the type locality.

13. *Zyginama carapana*, n. sp. (Figs. 2O, 15)

Description. Length of male 3.3 mm. Pale yellow overall, unmarked except black scutellum apex and fuscous maculae at base and apex of forewing costal plaque. Head (Fig. 2O) narrower than pronotum; crown in dorsal view slightly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 15a) with dorsal appendage arising near midlength, not elevated above margin of lobe, acute, bent posteroventrad, extended nearly to apex of lobe; ventral appendage arising preapically, extended dorsomesad (broken in holotype); lobe between appendages rounded; ventrolateral setal group with ~5 enlarged setae. Aedeagus (Figs. 15b, c) with preatrium well developed, shorter than shaft; dorsal apodeme in lateral view strongly broadened dorsally; shaft in lateral view slender, evenly recurved; paired basal processes extended along sides of shaft to gonopore; apex compressed, bluntly rounded in lateral view, without processes; gonopore preapical on posterior surface.

Material examined. Holotype male, MEXICO, Michoacan, Carapan, km 432, 2 October

1941 (DeLong, Good, Caldwell); 1 male paratype, same data [INHS].
Notes. This species resembles *Z. munda* in coloration, but has the aedeagal shaft in lateral view more slender and rounded rather than angulate apically. The species name, an adjective, refers to the type locality.

14. *Zyginama tripunctata* (Beamer) (Figs. 2P, 16)
Erythroneura tripunctata Beamer, 1929b: 119
Zygina tripunctata, Young, 1952:76
Zyginama tripunctata, Dietrich & Dmitriev, 2006:150
Type locality: Oak Creek Canyon, Arizona [KU].
Distribution: USA: Arizona, Florida, Texas.
Notes: Length of male 3.4 mm, female 3.7 mm. Specimens from Florida, collected on *Quercus myrtifolia* [INHS] and identified as this species, are much paler overall than those from the southwestern USA but are considered to be conspecific because of the very similar male genitalia. This is the only species of the genus recorded from Florida.

15. *Zyginama coahuilensis*, n. sp. (Figs. 2Q, 17)
Description. Length of male 3.4 mm. Dull yellow overall, crown with pair of brown preapical spots and median apical spot, midline brown; pronotum with pair of submedial J-shaped red maculae; mesonotal triangles bright yellow; forewing with broad red streak in basal half of clavus and another in brachial cell. Head (Fig. 2Q) narrower than pronotum, crown in dorsal view with median length distinctly greater than length next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 17a) with dorsal appendage arising near midlength, long, straight, attenuate, not reaching pygofer apex; ventral process arising at apex, moderately long, slender, gently curved dorsomesad; lobe between appendages rounded, poorly sclerotized; ventrolateral setal group with ca. 4 conspicuous setae. Aedeagus (Figs. 17b, c) with preatrium well developed; shaft strongly compressed, broad and nearly parallel-sided in lateral view, gently curved, posterior margin minutely serrate, rounded near apex; pair of short triangular lateral projections just distad of gonopore; subbasal processes slender, extended two-thirds distance to shaft apex, slightly divergent in posterior view; gonopore preapical on posterior surface.
Material examined. Holotype male, MEXICO, Coahuila, Saltillo, 23 September 1941 (DeLong, Good, Caldwell, Plummer) [INHS].
Notes. This species resembles *Z. tripunctata* in coloration, but differs in having the aedeagal shaft broader in lateral view with a pair of small distal projections and the subbasal processes more slender. The species name, an adjective, refers to the type locality.

16. *Zyginama orizaba*, n. sp. (Figs. 2R, 18)
Description. Length of male 3.3 mm. Ground color pale yellow; head with small brown apical spot, crown with orange medial patch posteriorly; pronotum with pair of posteriorly divergent orange streaks; mesonotal triangles brown; scutellum apex black; forewing clavus with basal and medial orange spot, brachial cell with basal and medial red patch, vein M with three red areas alternating with those of brachial cell; apical cells and areas adjacent to costal plaque infused with brown; abdominal terga brown. Head (Fig. 2R) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 18a) with dorsal appendage arising near base, weakly elevated at base, bent posteroventrad, attenuate, extended to apex of lobe; ventral appendage arising at apex, short, extended posterodorsad; lobe between appendages rounded; ventrolateral setal group with ~5 enlarged setae. Aedeagus (Figs. 18b, c) without preatrium; dorsal apodeme in lateral view broadened dorsally; shaft slender, nearly straight; subbasal paired processes extended along sides of shaft to near gonopore, divergent from midlength in posterior view; preapical processes, broad, triangular, extended anterad; distal lobe compressed, bent at right angle to shaft, apex acute; gonopore preapical on posterior surface.
Material examined. Holotype male, MEXICO, Veracruz, Orizaba, km 260, 17 October 1941 (DeLong, Good, Caldwell, Plummer) [INHS].
Notes. This species resembles *Z. colima* in coloration but is readily distinguished by the elongate dorsal pygofer appendage and the rectangularly bent distal lobe of the aedeagus. The species name, an adjective, refers to the type locality.

17. *Zyginama rodmani,* n. sp. (Figs. 2S, 19)
Description. Length of male 3.9 mm. Ground color off white; face with apex of anteclypeus and antennal pit brown, with pair of small orange spots adjacent to eyes and median hourglass-shaped orange macula extended onto crown; crown with pair of orange blotches, each with obscure brown spot; pronotum with anterior margin broadly bordered with cream interrupted by submedian and lateral pairs of orange maculae; mesonotal triangles brown; scutellum apex brown; forewing clavus and discal cells with large irregular but symmetrical reddish blotches; meso- and metathoracic sterna and abdomen mostly brown. Head (Fig. 2S) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 19a) with dorsal appendage arising in basal half, attenuate, not elevated above pygofer margin, extended nearly to apex of lobe; ventral appendage arising near apex, short, extended dorsomesad; lobe between appendages rounded; ventrolateral setal group with ~4 enlarged setae. Aedeagus (Figs. 19b, c) without preatrium; in lateral view with dorsal apodeme broadened dorsad; shaft compressed, broadened and obliquely rounded apically; paired subbasal processes closely appressed to each other and little divergent from shaft, extended 2/3 distance to shaft apex; apex in posterior view acute with pair of short obtusangular preapical lateral flanges; gonopore preapical on posterior surface.
Material examined. Holotype male, MEXICO, 50 km E Mexico City, 29 December 1949 (R.H. Beamer) [OSU].
Note. This species is the only known *Zyginama* species whose color pattern includes numerous red flecks on the forewing. Other distinctive features include its large size and aedeagus with the apex expanded and broadly expanded in lateral view. The species is named in honor of Dr. James E. Rodman to recognize his advocacy and promotion of the science of systematic biology through many years of outstanding service as Program Director in the Division of Environmental Biology, National Science Foundation, Washington, DC, USA.

18. *Zyginama malleta*, n. sp. (Figs. 2T, 20)
Description. Length of male 3.5 mm (approximate). Ground color dull yellow; markings of head unknown (head missing in holotype); pronotum with brown spot near midlength of lateral margin; mesonotal triangles brown; apex of scutellum black; thoracic sterna and abdominal segments mostly brown; forewing infused with brown, with dull yellow streaks along longitudinal veins. Male pygofer (Fig. 20a) with dorsal appendage arising in basal half, slightly elevated above margin of lobe at base, elongate, slender, curved ventrad, apex blunt, not reaching apex of lobe; ventral appendage arising preapically, moderately long, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group with ~5 enlarged setae. Aedeagus (Figs. 20b, c) with preatrium short; dorsal apodeme in lateral view narrow, slightly expanded dorsad; shaft compressed, in lateral view moderately broad, with pair short triangular projections on dorsal margin near base; subbasal processes extended along sides of shaft 2/3 distance to apex, curved slightly posterad, divergent in posterior view; apex in lateral view with quadrate anterior lobe and clawlike posterior projection; gonopore apical.
Material examined. Holotype male, MEXICO, Michoacan, Carapan, km 432, 2 October 1941 (DeLong, Good, Caldwell, Plummer) [INHS].
Notes. This species resembles *Z. tripunctata* in coloration, but is readily distinguished by the distinctive hammerlike aedeagal apex, upon which the species name, an adjective, is based.

19. *Zyginama zitacuarensis*, n. sp. (Figs. 2U, 21)
Description. Length of male 3.4 mm. Ground color pale yellow; head unmarked; pronotum with pair of orange submedial stripes bent laterad posteriorly; mesonotal triangles pale orange; scutellum apex black; forewing clavus with broad orange longitudinal stripe, corium with orange stripe along vein Cu. Head (Fig. 2T) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin acutely angled. Male pygofer (Fig. 21a) with dorsal appendage arising in basal half, not elevated above margin of lobe, attenuate, curved slightly ventrad, extended nearly to apex of lobe; ventral appendage arising at apex, short, curved posterodorsad; lobe between appendages rounded; ventrolateral setal group with ~5 enlarged setae. Aedeagus (Figs. 21b, c) without preatrium; dorsal apodeme in lateral view expanded dorsally; shaft compressed, in lateral view nearly straight,

with pair of triangular processes dorsally near midlength, posterior margin irregularly serrate preapically, with preapical constriction; paired subbasal processes extended along sides of shaft 2/3 distance to apex, divergent in posterior view; distal processes absent; apical lobe subquadrate; gonopore preapical on posterior surface.

Material examined. Holotype male, MEXICO, Michoacan, Zitacuaro, 29 September 1941 (DeLong, Good, Caldwell, Plummer) [INHS].

Notes. This species resembles *Z. vittata* in coloration, but differs in having the scutellum black apically. The aedeagus resembles that of *Z. rodmani*, but differs in having a pair of dorsal preapical triangular processes and the apex no wider in lateral view than the width of the shaft at midlength. The species name, an adjective, refers to the type locality.

20. *Zyginama rubrocta*, n. sp. (Figs. 2V, 22)

Description. Length of male 3.3 mm. Ground color pale yellow; crown red except along anterior margin; pronotum with broad red transverse band extended onto pleuron; mesonotum and scutellum red; forewing base red, with large nearly circular red transcommisural marking near midlength with anterior and posterior extensions to costal margin; mesosternum and abdominal terga dark brown. Head (Fig. 2V) narrower than pronotum, crown in dorsal view strongly produced medially, apex acutely angular. Male pygofer (Fig. 22a) with dorsal appendage arising near midlength, base slightly elevated above margin of lobe, acuminate, distal half bent ventrad, extended to apex of lobe; ventral appendage arising preapically, long, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group with ~6 slightly enlarged setae. Aedeagus (Figs. 22b, c) without preatrium; dorsal apodeme in lateral view slightly broadened dorsally; shaft in lateral view slender, slightly sinuate, with large unpaired basal process extended slightly beyond midlength and slightly divergent from shaft; paired distal processes arising basad of gonopore, slender, extended ventrad then curved anterad; apical lobe compressed, apex rectangular; gonopore preapical on posterior surface.

Material examined. Holotype male, MEXICO, Chiapas, Finca Prusia, 4 December 1932 (M.F. 2872) [INHS].

Notes. This species closely resembles *Z. iguala* in coloration and in the form of the aedeagus, but differs in having the pygofer dorsal appendage abruptly bent ventrad near its midlength and in lacking a posterior preapical spine on the aedeagus. The species name, an adjective, was formed by combining "*rubr-*" meaning "red" with "*octa*" meaning "eight" and refers to the eight red markings on the dorsum of this species.

21. *Zyginama iguala* (Ross) (Figs. 2W, 23)
Erythroneura iguala Ross, 1965a: 263
Zyginama iguala, Dietrich & Dmitriev, 2006:150

Type locality: Iguala, Guerrero, Mexico [OSU].

Distribution. MEXICO: Guerrero.

Notes: Length of male 2.8 mm, female 3.0 mm.

22. *Zyginama novella* (Knull & Auten) (Figs. 2X, 24)
Erythroneura novella Knull & Auten, 1938a:536
Zygina novella, Young, 1952:76
Zyginama novella, Dietrich & Dmitriev, 2006:150

Type locality: Chiricahua Mts., Arizona [OSU].

Distribution: USA: Arizona.

Notes: Length of male 3.0 mm, female 3.1 mm.

23. *Zyginama arizonica* (Knull & Auten) (Figs. 2Y, 25)
Erythroneura arizonica Knull & Auten, 1938a:536
Zygina arizonica, Young, 1952:76
Zyginama arizonica, Dietrich & Dmitriev, 2006:149

Type locality: Huachuca Mts., Arizona [OSU].

Distribution: USA: Arizona.

Notes: Length of male 3.3 mm, female 3.8 mm.

24. *Zyginama elongata*, n. sp. (Figs. 2Z, 26)

Description. Length of male 3.3-3.4 mm. Ground color pale yellow; face pale, unmarked; crown with small apical brown spot; pronotum with pair of sublateral brown spots and large submedial triangles, posterior margin white; mesonotum with three longitudinal brown stripes; scutellum apex black; forewing clavus with orange longitudinal stripe constricted medially, brachial cell mostly orange in distal two-thirds, costal cell yellow in basal two-thirds,

hyaline distally; mesosternum and abdomen except subgenital plates brown. Head (Fig. 2Z) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 26a) with dorsal appendage arising near base, acute, nearly straight, not elevated above pygofer margin, extended slightly beyond midlength of lobe; ventral appendage arising at apex of lobe, short, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group with ~6 enlarged setae. Aedeagus (Figs. 26b, c) without preatrium; in lateral view with dorsal apodeme slightly broadened dorsally; shaft in lateral view nearly straight, slender, broadened distally; paired subbasal processes extended beyond shaft midlength, slightly divergent from each other and from shaft; pair of elongate slender apical processes extended ventrolaterad with apices curved posterad; apex compressed, in lateral view rounded with anterior margin angled, notched posteriorly at gonopore; gonopore preapical on posterior surface.

Material examined. Holotype male, MEXICO, Morelos, 10 km N Cuernavaca, 28 December 1948 (R.H. Beamer) [OSU].

Notes. This species resembles *Z. aucta* in coloration but differs in having the aedeagus with paired basal and distal processes and the shaft apex broadened apically in lateral view. The species name, an adjective, refers to the elongate form of the body.

25. *Zyginama enigmata*, n. sp. (Figs. 2AA, 27)

Description. Length of male 3.5-3.7 mm, female 3.9 mm. Ground color pale yellow; face dull yellow medially, pale laterally; crown with pair of very diffuse brown preapical spots; pronotum dull yellow with arc of three pale blotches along anterior and lateral margins; posterior margin white; mesonotal triangles dull yellow; scutellum apex black; forewing mostly dull yellow with obscure fuscous markings, claval suture bordered with white; abdominal tergites brown. Head (Fig. 2AA) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 27a) with dorsal appendage arising in basal half, elevated above margin of lobe basally, curved ventrad then posterad and terminating in bluntly rounded tip, not reaching apex of lobe; ventral appendage arising preapically, long, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group with 1 enlarged seta. Aedeagus (Figs. 27b, c) with preatrium nearly as long as shaft; dorsal apodeme in lateral view short and broadly rounded; shaft in lateral view broad, compressed, arched posterodorsad; paired subbasal processes shorter than shaft, strongly divergent from shaft and each other; paired distal processes arising basad of gonopore, short, spinelike, extended basolaterad; apex compressed, abruptly bent dorsad; gonopore preapical on posteroventral surface.

Material examined. Holotype male, MEXICO, 50 km E Mexico City, 29 December 1949 (R.H. Beamer) [OSU]; 1 male and 2 female paratypes, same data [OSU].

Notes. This species resembles *Z. pinalensis, Z. inornata,* and *Z. brunnedorsum* in having the preatrium of the aedeagus elongate and the shaft broad and arcuate in lateral view, but differs in having a pair of large processes arising near the base of the shaft on the ventral side. The species name, an adjective, refers to the enigmatic shape of the aedeagus.

26. *Zyginama queretarensis*, n. sp. (Figs. 2BB, 28)

Description. Length of male 3.3 mm. Coloration similar to that of *Z. coahuilensis*, but brown spots larger and J-shaped maculae of pronotum broader and fused medially. Head (Fig. 2BB) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming obtuse angle. Pygofer (Fig. 28a) with dorsal appendage arising near midlength, not elevated above margin of lobe, short, broad, bent posteroventrad near midlength, apex blunt, not reaching apex of lobe; ventral appendage arising preapically, short, slender, extended dorsomesad; lobe between appendages rounded; ventrolateral setal group with ~4 enlarged setae. Aedeagus (Figs. 28b, c) with preatrium short; dorsal apodeme in lateral view broadened dorsally; shaft in lateral view, broad basally, abruptly narrowed from midlength to apex; with pair of rounded lateral subbasal flanges; with paired subbasal processes short, weakly divergent, extended slightly past midlength of shaft; paired distal processes arising adjacent to gononpore, somewhat flattened with obtusangular projection subbasally, curved ventrolaterad; apex compressed bent dorsad, obliquely rounded at tip; gonopore apical.

Material examined. Holotype male, MEXICO: Queretaro, Solis, 20 May 1928 (M.F. 1334) [INHS].
Notes. This species closely resembles *Z. tripunctata* in coloration, but differs in its distinctive male genitalia, including the bluntly rounded and ventrally bent dorsal pygofer appendage and the unique shape of the aedeagal apex. The species name, an adjective, refers to the Mexican state in which the holotype was collected.

27. *Zyginama obscura* (Beamer) (Figs. 2CC, 29)
Erythroneura obscura Beamer, 1929b: 117
Zygina obscura, Young, 1952:76
Zyginama obscura, Dietrich & Dmitriev, 2006:150
Type locality: Huachuca Mts., Arizona [KU].
Distribution: USA: Arizona.
Notes: Length of male 3.5 mm, female 3.8 mm.

28. *Zyginama angulata*, n. sp. (Figs. 2DD, 30)
Description. Length of male 3.3 mm. Ground color dull yellow; face brown except near dorsal margin; crown white with pair of diffuse orange submedial spots; pronotum with orange submedial triangles, posterior margin white; mesonotal triangles orange; scutellum apex black; forewing pale with orange longitudinal stripe in clavus and another along vein Cu; mesosternum and abdomen mostly dark brown. Head (Fig. 2DD) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 30a) with dorsal appendage arising near midlength, not elevated above margin of lobe, short, tapered to acute apex, curved ventrad, not extended to apex of lobe; ventral appendage apical, very short, toothlike; lobe between appendages rounded; ventrolateral setal group with ~4 enlarged setae. Aedeagus (Figs. 30b, c) without preatrium; dorsal apodeme in lateral view slender, slightly broadened dorsally; shaft in lateral view slender, slightly sinuate; paired subbasal processes elongate, slightly divergent from shaft, parallel to each other, extended to near gonopore; paired distal processes arising at apex, lamelliform with three branches, ventral pair arising from common stem and strongly divergent; gonopore apical.
Material examined. Holotype male, MEXICO, Distito Federal, Mexico City, Toluca Rd, 26 September 1945 (collector unknown) [INHS].
Notes. This species resembles *Z. triceroprocta* externally, but is readily distinguished by the very short ventral pygofer appendage and the distinctive, three-branched distal processes of the aedeagus. The species name, an adjective, refers to the angulate aedeagal processes.

29. *Zyginama durangensis*, n. sp. (Figs. 3A, 31)
Description. Length of male 2.9 mm. Ground color pale yellow; face without distinct markings; crown with weak pair of brown preapical spots and pair of longitudinal orange stripes extended onto pronotum and bent laterad near posterior margin at a 90° angle; mesonotal triangles pale orange; scutellum apex black; forewing veins orange, cells white; clavus with broad longitudinal orange stripe. Head (Fig. 3A) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 31a) with dorsal appendage arising in basal half, slightly elevated above margin of lobe, acuminate, curved ventromesad, not extended to apex of lobe; ventral appendage arising preapically, short, curved dorsad; lobe between appendages rounded ventrolateral setal group with ~3 enlarged setae. Aedeagus (Figs. 31b, c) without preatrium; dorsal apodeme in lateral view broadened dorsally; shaft compressed, in lateral view moderately broad, nearly straight, with pair of small dorsal basolateral lobes; subbasal paired processes weakly divergent from shaft in lateral view, extended to near gonopore; distal paired processes broad, lamelliform, with acuminate anteriorly directed apices; apex in lateral view slender, curved anterad, truncate, compressed; gonopore preapical on posterior surface.
Material examined. Holotype male, MEXICO, Durango, rt. 40 km 94 6.3km E El Salto, 23.83578°N, 105.32608°W, 2500m, 26 October 2005 (C.H. Dietrich) [INHS].
Notes. This species resembles *Z. agnata* in coloration and the structure of the male genitalia, but differs in having the distal processes of the aedeagus lamelliform and the shaft with a pair of short keels dorsally near the base. The species name, an adjective, refers to Mexican state in which the holotype was collected.

30. *Zyginama unicolor* (Beamer) (Figs. 3B, 32)
Erythroneura unicolor Beamer, 1929b:120

Zygina unicolor, Young, 1952:76
Zyginama unicolor, Dietrich & Dmitriev, 2006:150
Type locality: Culberson Co., Texas [KU].
Distribution: USA: Texas.
Notes: Length of male 3.3 mm, female 3.5 mm. Beamer's holotype [KU], the only known male of this species, has the genitalia dissected and mounted on a slide.

31. *Zyginama sola* (Knull & Auten) (Figs. 3C, 33)
Erythroneura sola Knull & Auten, 1938a: 534
Zygina sola, Young, 1952:76
Zyginama sola, Dietrich & Dmitriev, 2006:150
Type locality: Chiricahua Mts., Arizona [OSU].
Distribution: USA: Arizona.
Notes: Length of male 3.5 mm, female 3.7 mm. Knull and Auten (1938a) recorded oak as the host plant.

32. *Zyginama cornigera* (Beamer) (Figs. 3D, 34)
Erythroneura cornigera Beamer, 1937b: 31
Zygina cornigera, Young, 1952:75
Zyginama cornigera, Dietrich & Dmitriev, 2006:149
Type locality: Strawberry, California [KU].
Distribution: USA: California.
Notes: Length of male 3.0 mm, female 3.1 mm. This is the only known species of *Zyginama* that lacks a ventral pygofer appendage. Unlike species of other New World genera that lack this appendage, *Z. cornigera* has the ventolateral margin of the pygofer strongly sclerotized, suggesting a vestigial condition. As noted by Beamer (1937b) the apical processes of the aedeagus may be branched (as in the photo published by Beamer) or unbranched (as in Figs. 4T, U).

33. *Zyginama erosa* (McAtee) (Figs. 3E, 35)
Erythroneura erosa McAtee, 1924c: 36
Zygina erosa, Young, 1952:76
Zyginama erosa, Dietrich & Dmitriev, 2006:150
Type locality: Folsom, California [USNM].
Distribution: USA: California.
Notes: Length of male 2.8 mm, female 3.0 mm. The only known male specimens of this species, in Beamer's collection (KU), have the genitalia mounted on slides. Beamer (1932i) recorded this species from "live oaks".

34. *Zyginama casta* (Beamer) (Figs. 3F, 36)
Erythroneura casta Beamer, 1929b:118
Zygina casta, Young. 1952:75
Zyginama casta, Dietrich & Dmitriev, 2006:149
Type locality: Huachuca Mts. [east side of Car Peak near top], Arizona [KU].
Distribution: USA: Arizona.
Notes: Length of male 2.9 mm, female 3.3 mm. Beamer (1929b) recorded this species from "short, scrubby oaks".

35. *Zyginama agnata* (Knull & Auten) (Figs. 3G, 37)
Erythroneura agnata Knull & Auten, 1938a:537
Zygina agnata, Young, 1952:76
Zyginama agnata, Dietrich & Dmitriev, 2006:149
Type locality: Huachuca Mts., Arizona [OSU].
Distribution: USA: Arizona.
Notes: Length of male 2.8 mm, female 3.0 mm.

36. *Zyginama panamensis*, n. sp. (Figs. 3H, 38)
Description. Length of male 3.7 mm. Ground color pale yellow; head and pronotum without distinct markings; mesonotal triangles pale orange; scutellum apex black; forewing clavus with indistinct basal and medial male orange spots, costal area pale orange infused with brown, apical cells infused with brown. Head (Fig. 3H) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 38a) with dorsal appendage arising near base, not elevated above margin of lobe, attenuate, curved ventrad, extended slightly beyond midlength of lobe; ventral appendage arising at apex, moderately long, curved dorsomesad; lobe between appendages subquadrate; ventrolateral setal group with ~3 enlarged setae. Aedeagus (Figs. 38b, c) with preatrium short; dorsal apodeme in lateral view strongly expanded dorsally; shaft short, compressed, nearly straight, with short retrorse spine on dorsal margin near midlength; with single short asymmetrical process arising just basad of gonopore and curved ventrolaterad; paired processes absent; distal lobe com-

pressed, bluntly rounded; gonopore preapical on posterior surface.
Material examined. Holotype male, PANAMA: Chiriqui Pr., 4 km E Boquete Valle Palo Alto, 8°48'33"N, 82°23'59'W, 29 July 1999 (J. Shaffner) [TAMU].
Notes. This species resembles *Z. colima* in coloration but is paler overall and has distinctive male genitalia: the aedeagus has a retrorse preapical dorsal spine and an asymmetrical posterior preapical spine. The species name, an adjective, refers to the country in which the holotype was collected. This is the only *Zyginama* species recorded from Panama.

37. *Zyginama colima*, n. sp. (Figs. 3I, 39)
Description. Length of male 4.2 mm. Ground color pale yellow; head with small median brown apical spot, crown with pair of obscure orange submedial spots; pronotum with pair of orange submedial spots posteriorly; mesonotal triangles pale orange; scutellum apex black; forewing clavus with basal and medial orange maculae, corium with orange maculae at midlength and apex of brachial cell. Head (Fig. 3I) narrower than pronotum, crown in dorsal view with median length distinctly greater than length next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 39a) with dorsal appendage arising near midlength, not elevated above margin of lobe, long, acuminate, curved slightly ventrad, extended to apex of lobe, with long slender spine arising laterally near midlength and curved slightly dorsad; ventral appendage arising preapically, long, curved dorsomesad; ventrolateral setal group with ~8 enlarged setae. Aedeagus (Figs. 39b, c) with preatrium very short; dorsal apodeme in lateral view expanded dorsally; shaft in lateral view slender, irregularly recurved, with pair of short triangular processes on dorsal margin near midlength and pair of short rounded processes ventrolaterally near base; posterior margin with serrate median flange; apical lobe compressed, digitiform in lateral view; gonopore preapical on posterior margin.
Material examined. Holotype male, MEXICO: Jalisco, rd. to Parque Nacional de Volcan de Colima 11 mi. W hwy. junct. 54 (near Atenquique), 11–12 July 1984 (Carroll, Schaffner, Friedlander) [TAMU].
Notes. This species is similar to *Z. erosa* in coloration, but is readily distinguished by the elongate spine on the dorsal pygofer appendage and the lack of paired processes on the aedeagus. The species name, an adjective, refers to the type locality.

38. *Zyginama lanceolata*, n. sp. (Figs. 3J, 40)
Description. Length of male 3.7 mm, female 3.9 mm. Ground color pale yellow; head and pronotum without distinct markings; mesonotum and scutellum brown; forewing clavus with bright red transcommisural ellipse, costal margin with brown macula just distad of brochosome field. Head (Fig. 3J) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 40a) with dorsal appendage arising near midlength, base not elevated above margin of lobe, acuminate, curved dorsomesad, not extended to apex of lobe; ventral appendage arising at apex, very short; lobe between appendages shallowly concave; ventrolateral setal group conspicuous, but setae not enlarged. Aedeagus (Fig. 40b) without preatrium; dorsal apodeme short; shaft in lateral view straight, compressed, without paired processes, with short retrorse spine near midlength; apex acute, compressed, with short projection just basad of gonopore; gonopore preapical on posterior surface.
Material examined. Holotype male, MEXICO, 50 km E Mexico City, 29 December 1949 (J.G. Shaw) [OSU].
Notes. This species has a prominent orange macula on the forewing clavus similar to that of *Z. ritana*, but differs in having the mesonotum and scutellum entirely dark brown and in the distinctive lanceolate aedeagus, upon which the species name, an adjective, is based.

39. *Zyginama tricolor* (Beamer) (Figs. 3K, 41)
Erythroneura tricolor Beamer, 1929b: 124
Zygina tricolor, Young, 1952:76
Zyginama tricolor, Dietrich & Dmitriev, 2006:150
Type locality: Huachuca Mts. [east side of Car Peak], Arizona [KU].
Distribution: MEXICO: Distrito Federal. USA: Arizona.
Notes: Length of male 3.0 mm, female 3.2 mm. Beamer (1929b) recorded oak as the host.

40. *Zyginama tolteca*, n. sp. (Figs. 3L, 42)
Description. Length of male 3.2 mm, female 3.3 mm. Ground color dull yellow. Face dark

brown except dorsal margin; crown white with small apical spot and large posterior submarginal blotch orange. Pronotum with pair of lateral submarginal and anterior submedial orange spots in some cases merging with larger median posteior orange area; posteiror margin white. Mesonotal triangles orange-brown; scutellum apex black. Forewing basal two-thirds orange red with two large transcommisural white areas in clavus; costal plaque white; apical cells except third smoky. Mesosternum and abdominal terga brown. Head (Fig. 3L) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 42a) with dorsal appendage arising in basal half, elevated above margin of lobe, nearly straight, acuminate, extended slightly beyond apex of lobe; ventral appendage arising preapically, elongate, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group conspicuous but with setae only slightly enlarged. Aedeagus (Figs. 42b, c) with preatrium well developed, shorter than shaft; dorsal apodeme in lateral view tapered to abruptly broadened apex; shaft recurved, slender, apex compressed, without processes; gonopore preapical on posterior surface.

Material examined. Holotype male, MEXICO, Morelos, 10 km N Cuernavaca, 28 December 1948 (R.H. Beamer) [OSU]; 1 female paratype, same data [OSU].

Notes. This species resembles *Z. olmeca* in coloration but has the orange bands and spots more broken and irregular, the dorsal appendage of the pygofer nearly straight, and the aedeagal shaft lacking paired processes. The species name, an adjective, is based on that of the Toltec pre-Columbian culture of Mexico.

41. *Zyginama nuda* (Knull & Auten) (Figs. 3M, 43)

Erythroneura nuda Knull & Auten, 1938a:538

Zygina nuda, Young, 1952:76

Zyginama nuda, Dietrich & Dmitriev, 2006:150

Type locality: Santa Rita Mts., Arizona [OSU].

Distribution: USA: Arizona.

Note: Length of male 3.0 mm, female 3.4 mm. The holotype [OSU] is the only known male. The genitalia are mounted on a slide and appear to be damaged.

42. *Zyginama brunnedorsum*, n. sp. (Figs. 3N, 44)

Description. Length of male 3.3 mm, female 3.6 mm. Ground color pale yellow; face bright yellow, without dark markings; dorsum with broad dark brown marking covering entire crown and pronotum except lateral margins, mesonotum and scutellum, and extended obliquely across middle of forewing clavus to costal margin; a second broad oblique brown band extended across distal crossveins. Head (Fig. 3N) narrower than pronotum; crown in dorsal view strongly produced medially, anterior margin forming acute angle. Male pygofer (Fig. 44a) with dorsal appendage arising near midlength, elevated above margin of lobe basally, curved ventrad then posterad, apex acuminate, not extended to apex of lobe; ventral appendage arising apically, moderately long, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group conspicuous but setae not enlarged. Aedeagus (Figs. 44b, c) with preatrium well developed, shorter than shaft; dorsal apodeme in lateral view broadly rounded; shaft in lateral view broad, compressed, arched posterodorsad; without subbasal processes; paired spines arising on dorsal margin slightly beyond midlength and extended basad along shaft; pair of apical processes arising near apex ventrad of gonopore; pair of short triangular flanges on ventral margin just basad of gonopore; apex in lateral view with slender process extended dorsad at right angle to shaft and distal process arising ventrad of gonopore and extended distad; gonopore apical.

Material examined. Holotype male, MEXICO, 50 km E Mexico City, 29 December 1949 (R.H. Beamer); 1 male and 1 female paratype, same data [OSU].

Notes. The color pattern of this species, which resembles that of the temperate North American erythroneurine species *Erythridula juglandacea* (Ross & DeLong), is unique among known *Zyginama* spp. The aedeagus resembles that of *Z. pinalensis* but differs in having the distal spine straight and the ventroapical processes extended posteroventrad. The species name, a noun in apposition, refers to the brown coloration of the dorsum.

43. *Zyginama pinalensis* (Beamer) (Figs. 3O, 45)

Erythroneura pinalensis Beamer, 1929b: 119

Zygina pinalensis, Young, 1952:76
Zyginama pinalensis, Dietrich & Dmitriev, 2006:150
Type locality: Pinal Co., Arizona [KU].
Distribution. USA: Arizona.
Notes: Length of male 2.8 mm, female 3.0 mm.

44. *Zyginama triceroprocta* (Beamer) (Figs. 3P, 46)
Erythroneura triceroprocta Beamer, 1929b:118
Zygina triceroprocta, Young, 1952:76
Zyginama triceroprocta, Dietrich & Dmitriev, 2006:150
Type locality: Culberson Co., Texas [KU].
Distribution: USA: Texas.
Notes: Length of male 3.2 mm, female 3.5 mm.

45. *Zyginama multifurca*, n. sp. (Figs. 3Q, 47)
Description. Length of male 3.7 mm, female 3.5 mm. Ground color dull yellow; face pale, unmarked; crown with median apical and pair of preapical brown spots; pronotum with indistinct pair of orange submedial triangles, posterior margin white; mesonotal triangles orange; scutellum apex black; forewing hyaline with longitudinal yellow-orange stripe in clavus and another along vein Cu; mesosternum and abdominal tergites brown. Head (Fig. 3Q) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 47a) with dorsal appendage arising near midlength, short, broad, elevated slightly above margin of lobe, apex shallowly bifid with preapical ventral spine, not extended to apex of lobe; ventral appendage arising preapically, short, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group with ~8 enlarged setae. Aedeagus (Figs. 47b, c) without preatrium; dorsal apodeme in lateral view slender, nearly parallel-sided; shaft in lateral view slender, elongate, recurved, broadened preapically; subbasal processes absent; paired distal processes slender, flattened, forked preapically with ventral branch shorter than dorsal, curved ventrolaterad then anterad; apex in lateral view attenuate with blunt tip, in posterior view trifurcate; gonopore preapical on posterior margin.
Material examined. Holotype male, MEXICO, 50 km E Mexico City, 29 December 1949 (R.H. Beamer) [OSU]; 2 female paratypes, same data.
Notes. This species resembles *Z. tripunctata* in coloration, but is readily distinguished by the male genitalia. The dorsal pygofer appendage is broad and tridentate, and the aedeagus is also tridentate distally with a pair of bifid preapical processes. The species name, an adjective, refers to the forked aedeagal processes.

46. *Zyginama colorada*, n. sp. (Figs. 3R, 48)
Description. Length of male 3.6 mm. Ground color pale yellow with obscure orange markings; forewing veins orange, cells white; clavus with broad longitudinal orange stripe. Head (Fig. 3R) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 48a) with dorsal appendage arising in basal half, elevated above margin of lobe, acuminate, curved ventrad then posterad, not extended to apex of lobe; ventral appendage arising preapically, long, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group with ~2 enlarged setae. Aedeagus (Figs. 48b, c) with preatrium well developed, nearly as long as shaft; dorsal apodeme in lateral view broadly rounded; shaft in lateral view straight, slender, compressed, with pair of dorsal subbasal spines and pair of slender preapical processes curved ventrolaterad; apex with elongate digitiform lobe extended posterodorsad and short ventral spine extended ventrad; gonopore apical.
Material examined. Holotype male, USA, Colorado, Green Mt. Falls, el. 8000 ft., 25 August 1954 (Ross and Ross) [INHS]; 1 male paratype labeled "Colorado" [CSU].
Notes. This species closely resembles *Z. utahna*, but differs in having the dorsal pygofer appendage footlike and the aedeagus lacking dorsal preapical spines. The species name, an adjective, refers to the type locality.

47. *Zyginama vittata*, n. sp. (Figs. 3S, 49)
Description. Length of male 3.3 mm. Pale yellow overall, crown without brown spots, with obscure U-shaped orange macula extended onto pronotum; forewing with longitudinal orange vittae on clavus and along vein Cu. Head (Fig. 3S) slightly narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 49a) with dorsal appendage arising near midlength, slightly elevated above margin of lobe, short, acuminate, bent

ventrad, not extended to apex of lobe; ventral appendage slender, moderately long, extended dorsomesad; lobe between appendages nearly straight; ventrolateral setal group with ~2 conspicuous setae. Aedeagus (Figs. 49b, c) with preatrium nearly as long as shaft; dorsal apodeme in lateral view very large, quadrate anteriorly, broadly rounded posteriorly; shaft in lateral view slender, straight; without basal processes; pair of distal processes arising adjacent to gonopore, twisted anterolaterad, bifid apically; apical lobe bent at right angle to shaft, attenuate, tip hooked with pair of short lateral processes; gonopore apical.

Material examined. Holotype male, MEXICO: Michoacan, Uruapan, 1 October 1941 (DeLong, Good, Caldwell, Plummer) [INHS].

Notes. This species resembles *Z. colorada* in coloration and in the male genitalia, but is readily distinguished by the aedeagus, which lacks dorsal preapical spines and an unpaired ventral spine distally, and has the paired distal processes forked distally and the shaft apex strongly hooked in lateral view. The species name, an adjective, refers to the yellow vittae on the crown and forewing.

48. *Zyginama cimarroni* (Beamer) (Figs. 3T, 50)
Erythroneura cimarroni Beamer, 1929b: 119
Zygina cimarroni, Young, 1952:75
Zyginama cimmaroni, Dietrich & Dmitriev, 2006:149

Type locality: Colfax Co., New Mexico [KU].

Distribution: USA: New Mexico.

Notes: Length of male 3.7 mm, female 3.8 mm.

49. *Zyginama inornata* (McAtee) (Figs. 3U, 51)
Erythroneura inornata McAtee, 1924d:132
Zygina inornata, Young, 1952:76
Zyginama inornata, Dietrich & Dmitriev, 2006:150

Type locality: Ward, Colorado [USNM].

Distribution: USA: Arizona, Colorado.

Notes: Length of male 3.5 mm, female not seen. The concept of this species follows that of Beamer, who compared his specimens to McAtee's holotype and whose collection contains a male specimen with the genitalia dissected and mounted on a slide [KU]. Beamer (1934c) recorded this species from *Ceonothus* sp.

50. *Zyginama utahna* (Beamer) (Figs. 3V, 52)
Erythroneura utahna Beamer, 1937b: 32
Zygina utahna, Young, 1952:76
Zyginama utahna, Dietrich & Dmitriev, 2006:150

Type locality: Cedar City, Utah [KU].

Distribution: USA: Utah.

Notes: Length of male 3.2 mm, female unknown. The genitalia of the holotype, the only known male, are dissected and permanently mounted on a slide [KU].

51. *Zyginama serrata*, n. sp. (Figs. 3W, 53)

Description. Length of male 4.1 mm. Ground color pale yellow; head apex with small black medial spot; pronotum with pair of obscure yellow submedial spots; forewing with yellow streak near middle of anal vein, short yellow streaks near midlength and apex of vein Cu. Head (Fig. 3W) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 53a) with dorsal appendage arising in basal half, elevated above and strongly divergent from dorsal margin of lobe, elongate, gradually broadened to irregularly serrate tip, extended well beyond apex of lobe; ventral appendage arising at apex, long, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group inconspicuous. Aedeagus (Figs. 53b, c) with preatrium well developed, slender; dorsal apodeme in lateral view slender, slightly expanded dorsally; shaft strongly compressed, in lateral view very broad, irregularly ovoid; pair of slender processes arising near midlength basad of gonopore and curved slightly anterodorsad; ventral margin flared in posterior view; distal lobe compressed and bluntly rounded; gonopore preapical on posterior surface.

Material examined. Holotype male, MEXICO: Nuevo Leon, 5.5 mi. N La Ascencion, 8 July 1986 (Kovarik, Schaffner) [TAMU].

Notes. This species is most readily distinguished by its distinctive dorsal pygofer appendage, which has a truncate, serrate apex; and by the aedeagus, the shaft of which is very broad and nearly ovoid in lateral view. The species name, an adjective, refers to the serrate apex of the dorsal pygofer appendage.

52. *Zyginama spatulata*, n. sp. (Figs. 3X, 54)

Description. Length unknown (wings of holotype badly damaged). Ground color pale

yellow, unmarked except pale yellow longitudinal streak in clavus and along vein Cu of forewing, abdominal terga brown. Head (Fig. 3X) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 54a) with dorsal appendage arising near midlength, not elevated above margin of lobe, attenuate, sinuately curved posteroventrad, extended nearly to apex of lobe; ventral appendage arising preapically, moderately long, curved posterodorsad; lobe between appendages rounded; ventrolateral setal group with ~2 enlarged setae. Aedeagus (Figs. 54b, c) with preatrium nearly as long as shaft; dorsal apodeme in lateral view greatly expanded; shaft compressed, moderately narrow in lateral view, nearly straight; subbasal processes absent; distal processes arising anterolaterad of gonopore, short, acute, extended anterolaterad; distal lobe compressed, triangular in lateral view; gonopore preapical on posterior surface.
Material examined. Holotype male, MEXICO, Michoacan, Carapan, km 432, 2 October 1941 (DeLong, Good, Caldwell, Plummer) [INHS].
Notes. This indistinctively marked species is most readily distinguished by the broad triangular apex of the aedeagus, and by the dorsal pygofer appendage which is spatulate distally and upon which the species name, an adjective, is based.

53. *Zyginama ochrescens*, n. sp. (Figs. 3Y, 55)
Description. Length of male 2.8 mm. Ground color dull orange. Crown anterior margin and posterior pronotal margin white. Forewing basal two-thirds orange with large white spot at base of clavus, another at base of corium, and two on costal plaque; distal crossveins bordered in white; apical cells smoky. Head (Fig. 3Y) subequal in width to pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 55a) with dorsal appendage arising near midlength, elevated above margin of lobe, curved ventromesad, constricted preapically, apex bluntly rounded, extended to apex of lobe; ventral appendage arising at apex, long, curved dorsomesad; lobe between appendages nearly straight; ventrolateral setal group with ~3 enlarged setae. Aedeagus (Figs. 55b, c) with preatrium well developed, shorter than shaft; dorsal apodeme in lateral view parallel-sided; shaft slender, tubular, slightly recurved; subbasal processes absent; preapical paired processes slender, extended ventrad and curved slightly anterad; apex in lateral and posterior views attenuate, tip bluntly rounded; gonopore preapical on posterior surface.
Material examined. Holotype male, MEXICO "MF 2576" [OSU].
Notes. The holotype was apparently collected by A. Dampf. His field notes, housed in the C.A. Triplehorn Insect Collection at OSU and associated with the lot number on the holotype read as follows "31.V.1932. heat wave, last days without rain. Made on light using 300W bulb and special trap. Suburb of San Jacinta D. F. Mexico City (2240 m), surrounded by gardens and facing vegetable fields. Nearby trees are *Fraxinus*, *Salix*, & *Cupressus*. Collr. A. Dampf."
This species is readily distinguished by its nearly uniform dull orange coloration and distinctive distally rounded dorsal pygofer appendage. The species name, an adjective, refers to the orange coloration.

54. *Zyginama toluca*, n. sp. (Figs. 3Z, 56)
Description. Length of male 4.0-4.2 mm, female 3.8-4.0. Ground color dull yellow. Anteclypeus and lateral margin of frontoclypeus ventrad of antennal pit brown; crown orange medially with apical and pair of preapical brown spots. Pronotum, mesonotum and scutellum orange; scutellum apex black. Forewing basal two-thirds yellow orange; claval suture and median discal cell white; apical cells hyaline. Thoracic venter and abdomen dark brown with margins of sclerites pale. Head (Fig. 3Z) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 56a) with dorsal appendage arising in basal half, elevated above margin of lobe, acuminate, nearly straight, not extended to apex of lobe; ventral appendage arising at apex of lobe, short, extended dorsomesad; lobe between appendages nearly straight; ventrolateral setal group with ~9 enlarged setae. Aedeagus (Figs. 56b, c) without preatrium; dorsal apodeme in lateral view strongly broadened dorsally; shaft in lateral view straight through most of length, with medially humped dorsal keel; subbasal processes absent, with rounded lateral subbasal keel; paired distal processes arising adjacent to gonopore, slender, extended slightly ventrolaterad then curved anterodorsad,

with or without preapical tooth; apex in lateral view hooked anterad, trifurcate in posterior view; gonopore preapical on posterior surface.
Material examined. Holotype male, MEXICO: Mexico City, Toluca Rd., 26 October 1945 (collector unknown) [INHS]; 1 female paratype, same data [INHS]; 2 male and 1 female paratytpes, MEXICO, 50 km E Mexico City, 29 December 1949 (R.H. Beamer) [OSU]; 1 female paratype, MEXICO, Morelos, 10 km N Cuernavaca, 28 December 1948 (R.H. Beamer) [OSU].
Notes. This species has markings similar to those of *Z. tripunctata* but the dorsal coloration is more orange overall. The aedeagus, with its prominent anterodorsal hump and paired lateral distal flanges, is also distinctive. The species name, a noun in apposition, is based on that of the type locality.

55. *Zyginama pallescens*, n. sp. (Figs. 3AA, 57)
Description. Length of male 3.3 mm. Pale stramineous overall, crown without brown spots, forewing with longitudinal yellow vittae on clavus and along vein Cu. Head (Fig. 3AA) slightly narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 57a) with dorsal appendage arising near midlength, not elevated above margin of lobe, short, acuminate, curved ventrad; ventral appendage arising at apex, short, slender, curved dorsomesad; lobe between appendages rectangular; ventrolateral setal group with ~2 enlarged setae. Aedeagus (Figs. 57b, c) with preatrium well developed, shorter than shaft; dorsal apodeme in lateral view very large, subquadrate; shaft compressed, in lateral view moderately broad, nearly straight; subbasal processes absent; paired distal processes short, slender, arising adjacent to gonopore, curved anteroventrad; apex truncate in lateral view, bifid in posterior view, two sides compressed; gonopore apical.
Material examined. Holotype male, MEXICO: Michoacan, Carapan, km 432, 2 October 1941 (DeLong, Good, Caldwell, Plummer) [INHS].
Notes. This species is most easily distinguished by the aedeagus, which has the shaft apex distinctly bifid in posterior view with a pair of short slender lateral processes. The species name, an adjective, refers to the pale coloration.

56. *Zyginama blanda* (Knull & Auten) (Figs. 3BB, 58)
Erythroneura blanda Knull & Auten, 1938a:538
Zygina blanda, Young, 1952:76
Zyginama blanda, Dietrich & Dmitriev, 2006:149
Type locality: Huachuca Mts., Arizona [OSU].
Distribution: USA: Arizona.
Notes: Length of male 3.0 mm, female 3.3 mm.

57. *Zyginama pallenta* (Beamer) (Figs. 3CC, 59)
Erythroneura pallenta Beamer, 1929b:117
Zygina pallenta, Young, 1952:76
Zyginama pallenta, Dietrich & Dmitriev, 2006:150
Type locality: Oak Creek Canyon, Arizona [KU].
Distribution: USA: Arizona.
Notes: Length of male 3.8 mm, female 3.8 mm.

58. *Zyginama olmeca*, n. sp. (Figs. 3DD, 60)
Description. Length of male 3.8 mm, female 3.8 mm. Ground color dull yellow. Face with dorsal submarginal brown transverse band extended across eye and thoracic pleuron, continuing along costal margin of forewing. Crown off-white, with large median red-orange spot extended to posterior margin. Pronotum off-white with large median red-orange triangle with narrow part extended to posterior margin. Mesonotum brown except median pale area; scutellum apex black. Forewing mostly reddish in basal two-thirds with large oblique ovoid white area near base and more elongate white area distad; inner and outer apical cells brown, third white. Venter and abdominal terga pale. Head (Fig. 3DD) narrower than pronotum; crown in dorsal view distinctly longer medially than next to eye, anterior margin forming 90° angle. Male pygofer (Fig. 60a) with dorsal appendage arising in basal half, elevated above margin of lobe, slender, curved ventromesad, not extended to apex of lobe; ventral appendage arising at apex, short, extended mesad; lobe between appendages shallowly concave; ventrolateral setal group with ~3 enlarged setae. Aedeagus (Figs. 60b, c) without preatrium; dorsal apodeme in lateral view broadened dorsally; shaft in lateral view recurved, compressed in distal half; without subbasal processes; with pair of long slender preapical processes arising basad of gonopore, extended anteroventrad and

curved dorsad; apex acute; gonopore preapical on posterior surface.
Material examined. Holotype male, MEXICO, Morelos, 10 km N Cuernavaca, 28 December 1948 (R.H. Beamer) [OSU]; 2 female paratypes, same data.
Notes. This species is readily distinguished by its unique color pattern and male genitalia. The species name, an adjective, is derived from that of the Olmec culture, which inhabited southern Mexico from 1200-400 BCE.

59. *Zyginama ternaria* (Van Duzee) (Fig. 3EE)
Erythroneura ternaria Van Duzee, 1924a:232
Zygina ternaria, Young, 1952:76
Zyginama ternaria, Dietrich & Dmitriev, 2006:150
Type locality: Mill Creek Canyon, San Bernardino Co., California [CAS].
Distribution: USA: California.
Notes: Length of female 3.4 mm, male unknown. Van Duzee's holotype (Fig. 3EE) is a female. No other specimens are known. The dorsal color pattern, consisting of a pair of bold red subparallel longitudinal stripes extended from the crown to the forewing clavus and converging to the commisural margin distally, will separate it from all other known species. Because the coloration of this species differs considerably from that of all other known New World Erythroneurini, placement of this species in *Zyginama* must be considered tentative until males are discovered.

South American Species
The following species will key to (or near) *Zyginama* in the key to New World genera provided by Dietrich and Dmitriev (2006) but differ considerably from the North American species of the genus in external morphology. As in North American *Zyginama* species, these South American species have a simple, footlike style apex and well developed dorsal and ventral appendages on the male pygofer, but lack a macroseta at the base of the dorsal pygofer appendage (except *Z. intermedia*, n. sp.) and have the pair of spots on the crown absent or poorly delimited, excluding them from *Neozygina* Dietrich & Dmitriev. The only other described South American erythroneurine genera that have a ventral pygofer appendage are *Hamagina* Dietrich & Dmitriev and *Spinigina* Dietrich & Dmitriev, but *Hamagina* species have an unpaired dorsal process between the base of the aedeagus and the gonopore-bearing shaft, and *Spinigina* species have the first segment of the male anal tube spinose. Nevertheless, in the structure of the head (not or only weakly produced and as wide or wider than the pronotum) and forewing (second apical cell broad), most of the species described below resemble these and other genera of endemic South American Erythroneurini described by Dietrich and Dmitriev (2006), including also *Amazygina* and *Napogina*, known species of which lack a ventral pygofer appendage. The coloration of these species also resembles that of the various endemic South American genera in that the forewings lack a distinct color pattern and the overall coloration is white or pale yellow with various amounts of dark brown pigmentation (cf. Dietrich and Dmitriev (2006), Figs. 2P–R). Therefore, although they fit the current definition of *Zyginama* (Dietrich and Dmitriev 2006), the placement of these species in *Zyginama* is here considered provisional. Recognition of new genera or expansion of the concepts of previously described genera may become warranted as the erythroneurine fauna of South America becomes better known.

Key to South American Species Provisionally Placed in *Zyginama*

1 Aedeagus with conspicuous spicules or serrations posteroventrally (Figs. 62b, 65b)....2
1' Aedeagus with posteroventral surface smooth....6

2(1) Aedeagus with pair of long slender processes arising well distad of gonopore and curved anteroventrad (Fig. 62b, c)....3
2' Aedeagus without paired processes....5

3(2) Aedeagus with one pair of processes (Fig. 61c)....60. *Z. gibba*, n. sp.
3' Aedeagus with two pairs of processes (Fig. 62c)....4

4(3) Pygofer with dorsal appendage very long and slender, extended beyond apex of lobe, without preapical tooth (Fig. 62a); aedeagus with paired preapical processes extended dorsad (Fig. 62b).... ....61. *Z. longispina*, n. sp.
4' Pygofer with dorsal appendage short, not extended to apex of lobe, with preapical ventral tooth (Fig. 63a); aedeagus with paired preapical processes extended ventrad (Fig. 63b) ....62. *Z. tambopatensis*, n. sp.

5(2) Pygofer dorsal appendage furcate (Fig. 64a) ....63. *Z. furca*, n. sp.
5' Pygofer dorsal appendage truncate apically (Fig. 65a).... 64. *Z. spiculata*, n. sp.

6(1) Aedeagal shaft with two pairs of lateral processes (Fig. 67c) or with a single pair of branched processes (Fig. 68c) 7
6' Aedeagal shaft with one pair of unbranched lateral processes 10

7(6) Paired processes of aedeagus separate at base (Fig. 67c) 8
7' Paired processes of aedeagus branched distally (Fig. 68c)....9

8(7) Both pairs of aedeagal processes distinctly preapical, distal pair short and triangular (Fig. 66c) ....65. *Z. cristata*, n. sp.
8' Both pairs of aedeagal processes arising at apex, distal pair slender, sinuate (Fig. 67b) ....66. *Z. elevata*, n. sp.

9(7) Aedeagal processes slender with two distal projections (Fig. 68c)..... 67. *Z. gracilifurca*, n. sp.
9' Aedeagal processes lamelliform, with three distal projections (Fig. 69c) ....68. *Z. intermedia*, n. sp.

10(6) Paired aedeagal processes short, triangular (Fig. 70c).... 69. *Z. adisi*, n. sp.
10' Paired aedeagal processes elongate 11

11(10) Aedeagus in posterior view with apex truncate or emarginate (Figs.71c, 72c)....12
11' Aedeagus in posterior view with apex acuminate (Fig. 74c) 13

12(11) Pygofer dorsal appendage, broad, emarginate apically (Fig. 71a); aedeagus bifid apically (Fig. 71c)....70. *Z. bifida*, n. sp.
12' Pygofer dorsal appendage acuminate (Fig. 72a) ; aedeagus truncate apically (Fig. 72c).... ....71. *Z. truncata*, n. sp.

13(11) Aedeagal shaft in lateral view broadest basad of gonopore, apex broader than preapical process (Fig. 73b).... 72. *Z. ortha*, n. sp.
13' Aedeagal shaft in lateral view broadest distad of gonopore, apex narrower than preapical process (Fig. 74b)....73. *Z. attenuata*, n. sp.

60. *Zyginama gibba*, n. sp. (Figs. 4A, 61)
Description. Length of male 3.0-3.2 mm. Ground color dull yellow, infused with brown; crown with large median brown area extended to apex; mesonotum and scutellum mostly brown except medially; mesosternum and abdominal terga brown. Head (Fig. 4A) in dorsal view subequal in width to pronotum, crown longer medialy than next to eye, anterior margin obtusely angulate. Male pygofer (Fig. 61a) with dorsal appendage arising near midlength, slightly elevated above lobe, short, curved mesad, not extended to lobe apex; ventral appendage arising apically, moderately long, bent mesad at 90° angle; ventrolateral setal group with ~5 enlarged setae. Aedeagus (Figs. 61b, c) with preatrium short; dorsal apodeme expanded; spicules absent; shaft compressed, broad in lateral view, apex acuminate, with pair of long slender flattened preapical processes curved ventrolaterad; gonopore posterior near midlength of shaft.
Material examined. Holotype male, ECUADOR, Orellana, 1km S Onkonegare Camp, Reserva Etnica Waorani, 00°39'10"S, 076°26'00"W, 7 October 1995, fogging terra firme forest (T.L. Erwin, et al., lot#1244) [USNM]; 1 male and 1 female paratype, same data except 26 June 1996, lot#1598 [INHS, USNM].
Notes. This species resembles species of *Hamagina* in having a diffuse median dark area on the crown, but is easily distinguished by its distinctive genitalia. The species name refers to the posteriorly gibbous aedeagal shaft.

61. *Zyginama longispina*, n. sp. (Figs. 4B, 62)
Description. Length of male 3.8 mm. Ground color dull yellow; crown with pair of diffuse brown submedial spots preapically; mesonotal triangles dark brown; meskatepisternum dark brown. Head (Fig. 4B) in dorsal view slightly broader than pronotum, crown slightly longer medially than next to eye, anterior margin evenly rounded. Male pygofer (Fig. 62a) with dorsal appendage straight, abruptly narrowed beyond basal third, elongate, extended beyond apex of lobe; ventral appendage arising preapically, elongate, slender, curved slightly mesad then gradually dorsolaterad. Aedeagus (Figs.62b, c) with preatrium short; dorsal apodeme well developed, weakly expanded dorsally; base spiculate ventrally; shaft compressed, broad basally, slender distally, with pair of long slender preapical processes curving anterolaterad and pair of long apical processes curving sinuately ventrad; gonopore near base of shaft on posteroventral surface, bordered by pair of triangular flanges.
Material examined. Holotype male, ECUADOR, Orellana, 1km S Onkonegare Camp, Reserva Etnica Waorani, 00°39'10"S, 076°26'00"W, 3 October 1996, fogging terra firme forest (T.L. Erwin, et al., lot#1738) [USNM].
Notes. This species is similar to *Z. adisi* in coloration, but is readily distinguished by the distinctive aedeagus and the strongly attenuate dorsal pygofer appendage, upon which the species name is based.

62. *Zyginama tambopatensis*, n. sp. (Figs. 4C, 63)
Description. Length of male 3.0 mm. Ground color pale yellow, crown with diffuse brown area medially, mesonotal triangles and mesepisternum dark brown. Head (Fig. 4C) in dorsal view slightly wider than pronotum, crown slightly longer medially than next to eye, anterior margin evenly rounded. Male pygofer (Fig. 63a) with dorsal appendage arising near midlength, elevated above lobe, short, straight, acute, with ventral preapical projection; ventral appendage arising preapically, long, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group with ~8 enlarged setae. Aedeagus (Figs. 63b, c) with preatrium short; dorsal apodeme crescent-shaped in lateral view; shaft in lateral view broad basally, nearly straight, with serrate ventrolateral flange, pair of slender ventrally directed processes laterad of gonopore, and pair of long slender apical processes curved anteroventrad; gonopore preapical on posterior surface.
Material examined. Holotype male, PERU, Madre de Dios, Rio Tambopata Res., 30km (air) SW Pto. Maldonado, 290m, 12°50'S, 069°17'W, Smithsonian Institution Canopy Fogging Project, 4 May 1984 01/03/69 (T.L. Erwin, et al.) [USNM].
Notes. This species closely resembles *Z. longispina* but is readily distinguished by the short, bifid dorsal pygofer appendage and the ventrally directed preapical processes of the aedeagus. The species name refers to the type locality.

63. *Zyginama furca*, n. sp. (Figs. 4D, 64)
Description. Length of male 2.9 mm. Ground

color pale yellow; crown unmarked; mesonotal triangles light orange-brown. Head (Fig. 4D) in dorsal view subequal in width to pronotum, crown longer medially than next to eye, anterior margin obtusely angulate. Male pygofer (Fig. 64a) with dorsal appendage greatly enlarged, arising in basal half, elevated and strongly divergent from margin of lobe; branched near midlength, branches acuminate, both extended slightly beyond apex of lobe; ventral appendage arising preapically, moderately long, curved dorsomesad; lobe between appendages with prominent hump; ventrolateral setal group with ~6 enlarged setae. Aedeagus (Figs. 64b, c) with preatrium short; dorsal apodeme in lateral view broadly rounded; shaft very broad and strongly compressed, with pair of lamelliform lateral flanges; posterior margin irregularly serrate; processes absent; gonopore apical.

Material examined. Holotype male, PERU, Madre de Dios, Rio Tambopata Res., 30km (air) SW Pto. Maldonado, 290m, 12°50'S, 069°17'W, Smithsonian Institution Canopy Fogging Project, 8 November 1983 04/01/147 (T.L. Erwin, et al.) [USNM].

Notes. This species is similar externally to *Z. cristata*, but is readily distinguished by its massive forked dorsal pygofer appendage and short, broad, posteriorly serrate aedeagus. The species name refers to the forked pygofer appendage.

64. *Zyginama spiculata*, n. sp. (Figs. 4E, 65)

Description. Length of male 3.2 mm. Ground color pale yellow, unmarked. Head (Fig. 4E) in dorsal view subequal in width to pronotum, crown slightly longer medially than next to eye, anterior margin evenly rounded. Male pygofer (Fig. 65a) with dorsal appendage arising in basal half, elevated and arcuate above lobe, slender, slightly expanded distally, extended slightly beyond lobe, apex truncate and indistinctly crenulate; ventral appendage arising preapically, short, curved dorsad; ventrolateral setal group with ~6 slightly enlarged setae. Aedeagus (Figs. 65b, c) with preatrium well developed; dorsal apodeme in lateral view parallel sided; shaft short, with compressed dorsal lobe and pair of large denticulate ventrolateral flanges; gonopore preapical on posterior surface.

Material examined. Holotype male, PERU, Madre de Dios, Rio Tambopata Res., 30km (air) SW Pto. Maldonado, 290m, 12°50'S, 069°17'W, Smithsonian Institution Canopy Fogging Project, 8 November 1983 04/01/147 (T.L. Erwin, et al.) [USNM].

Notes. This species is similar to *Z. furca*, but is most easily distinguished by the form of the pygofer dorsal appendage, which is not forked but truncate and weakly crenulate distally. The species name refers to the spiculate aedeagus.

65. *Zyginama cristata*, n. sp. (Figs. 4F, 66)

Description. Length of male 3.1-3.2 mm, female 3.1 mm. Ground color pale yellow; crown unmarked; mesonotal triangles dark brown. Head (Fig. 4F) in dorsal view subequal in width to pronotum, crown longer medially than next to eye, anterior margin evenly rounded. Male pygofer (Fig. 66a) with dorsal appendage arising near base, elevated above margin of lobe, long, acuminate, curved ventrad, extended nearly to apex of lobe; ventral appendage arising preapically, long, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group with ~4 enlarged setae. Aedeagus (Figs. 66b, c) without preatrium; dorsal apodeme in lateral view slightly broadened dorsally; shaft slender, slightly recurved, without basal processes; with two pairs of distal processes arising preapically, one pair arising just basad of gonopore, slender, elongate, extended ventrolaterad then curved anterodorsad; other pair arising laterad of gonopore, short, triangular; apical lobe compressed, bluntly rounded in lateral view; gonopore preapical on posterior surface.

Material examined. Holotype male, ECUADOR, Orellana, 1km S Onkonegare Camp, Reserva Etnica Waorani, 00°39'10"S, 076°26'00"W, 10 February 1999, fogging terra firme forest (T.L. Erwin, et al., lot#976) [USNM]; 2 female paratypes, same data; 1 male paratype, same data except 30 September 1996, lot#1665 [INHS]; 1 male paratype, same data except 4 October 1995, lot #1176 [USNM].

Notes. This species is somewhat similar to *Z. attenuata* externally, but is readily distinguished by its distinctive aedeagus. The species name refers to the crested aedeagal apex.

66. *Zyginama elevata*, n. sp. (Figs. 4G, 67)

Description. Length of male 3.2 mm. Ground color dull yellow, heavily marked with brown; face except frontoclypeus medially, gena, and

lora brown; crown brown except pair of pale oblique marginal areas and pair of obscure black preapical spots brown; pronotum brown; mesonotum and scutellum mostly brown; forewing brown; mesosternum and abdominal terga dark brown. Head (Fig. 4G) in dorsal view broader than pronotum, crown no longer medially than next to eye, anterior margin broadly rounded. Male pygofer (Fig. 67a) with dorsal appendage arising near midlength, elevated and strongly divergent from margin of lobe, short, acuminate, curved posteroventrad, not extended to apex of lobe; ventral appendage arising preapically, long, curved dorsomesad; lobe between appendages with prominent hump; ventrolateral setal group with ~5 enlarged setae. Aedeagus (Figs. 67b, c) with preatrium short; dorsal apodeme in lateral view slender, slightly broadened dorsally; shaft in lateral view elongate, slender, slightly sinuate, with short retrorse spine near midlength of dorsal margin; basal processes absent; with two pairs of short, slender distal processes, one arising preapically, extended ventrad and curved slightly anterad; the other arising at apex, arched laterad and curved posteroventrad; apical lobe absent; gonopore apical.

Material examined. Holotype male, ECUADOR, Orellana, 1km S Onkonegare Camp, Reserva Etnica Waorani, 00°39'10"S, 076°26'00"W, 2 July 1995, fogging terra firme forest (T.L. Erwin, et al., lot#1067) [USNM].

Notes. The mostly dark brown coloration of this species is unique among known South American Erythroneurini, and the male genitalia are also distinctive. The species name refers to the elevated distal pair of aedeagal processes.

67. *Zyginama gracilifurca*, n. sp. (Figs. 4H, 68)

Description. Length of male 3.1 mm. Ground color dull yellow, infused with brown; crown with pair of diffuse brown submedial spots preapically; mesonotum and scutellum dark brown; mesosternum and abdominal terga dark brown. Head (Fig. 4H) in dorsal view subequal to pronotum in width, crown slightly longer medially than next to eye, anterior margin evenly rounded. Male pygofer (Fig. 68a) with dorsal appendage arising near midlength, not elevated above margin of lobe, acuminate, straight, extended nearly to apex of lobe; ventral appendage long, curved dorsomesad; lobe between appendages parabolically rounded; ventrolateral setal group conspicuous but setae not enlarged. Aedeagus (Figs. 69b, c) without preatrium; dorsal apodeme in lateral view nearly parallel-sided; shaft in lateral view very slender, elongate, slightly recurved, without basal processes; with pair of distal processes arising well basad of gonopore, extended ventrad then curved anterolaterad, shallowly forked apically; distal lobe compressed, acuminate in lateral view; gonopore preapical on posterior surface.

Material examined. Holotype male, ECUADOR, Orellana, 1km S Onkonegare Camp, Reserva Etnica Waorani, 00°39'10"S, 076°26'00"W, 30 September 1996, fogging terra firme forest (T.L. Erwin, et al., lot#1667) [USNM].

Notes. This species is similar to *Z. adisi* externally, but is easily identified by the aedeagus, the very slender shaft and forked preapical processes of which are distinctive and upon which the species name is based.

68. *Zyginama intermedia*, n. sp. (Figs. 4I, 69)

Description. Length of male 3.1 mm. Ground color pale yellow, crown and pronotum heavily infused with brown, mesonotal triangles and mesepisternum dark brown. Head (Fig. 3I) in dorsal view subequal to pronotum in width, slightly longer medially than next to eye, anterior margin evenly rounded. Male pygofer (Fig. 8Y) with dorsal appendage arising near midlength, elevated above and divergent from dorsal margin of lobe, slender, nearly straight, extended nearly to apex of lobe, with 1-2 enlarged setae at base; ventral appendage arising at apex, short, extended posterodorsad; lobe between appendages nearly straight; ventrolateral setal group with ~6 enlarged setae. Aedeagus (Figs. 8Z, AA) without preatrium; dorsal apodeme in lateral view strongly expanded dorsally; shaft compressed, in lateral view moderately broad, slightly recurved, without basal processes; paired distal processes arising adjacent to gonopore, lamelliform, with two short ventral preapical projections and elongate distal spine curved anterodorsad; distal lobe compressed, bluntly rounded in lateral view; gonopore preapical on posterior surface.

Material examined. Holotype male, PERU, Madre de Dios, Rio Tambopata Res., 30km (air) SW Pto. Maldonado, 290m, 12°50'S, 069°17'W, Smithsonian Institution Canopy Fogging Project, 14 September 1984 01/02/61 (T.L. Erwin, et al.) [USNM].

Notes. This species resembles *Z. gibba* in coloration. The presence of enlarged setae near the base of the dorsal pygofer appendage is a trait shared with species of the New World genus *Neozygina*. Nevertheless, other aspects of the morphology of this species, including the presence of enlarged setae in the ventrolateral setal group and the absence of distinct preapical spots on the crown indicate that the species is not closely related to *Neozygina*. The species name refers to the apparently intermediate position of this species between *Neozygina* and *Zyginama*.

69. *Zyginama adisi*, n. sp. (Figs. 4J, 70)
Description. Length of male 2.8 mm, female 2.9 mm. Ground color pale yellow; crown with pair of small brown submedial spots preapically; mesonotal triangles dark brown. Head (Fig. 4J) in dorsal view subequal to pronotum in width, crown longer medially than next to eye, anterior margin forming obtuse angle. Male pygofer (Fig. 70a) with dorsal appendage long, broadened, compressed, and slightly twisted preapically, apex attenuate, not extended to apical margin; ventral process arising near apex, slender, extended mesad; lobe between appendages subangulate; ventrolateral setal group with 5–8 conspicuous setae. Aedeagus (Figs. 70b, c) with preatrium well developed; dorsal apodeme strongly expanded in lateral view, pillarlike in posterior view; shaft tubular, slightly compressed, slender, with pair of short broad triangular processes preapically; gonopore apical.
Material examined. Holotype male, BRASIL, Amazonas, Hwy ZF 2, km 20.7, ca 60 km N Manaus, 02°30'S 060°15'W, 16 Aug 1979, terra firme; Canopy Fogging Project TRS#08, Tray #547, Adis, Erwin, Montgomery, et al.; 3 male, and 1 female paratypes, same data [USNM].
Notes. This species is very similar externally to several other South American Erythroneurini and is most readily identified by its distinctive male genitalia, e.g., the preapically expanded dorsal pygofer appendage and the slender aedeagal shaft with very short processes. The species is named in honor of the collector of the type series, Prof. Joachim Adis, who has made substantial contributions to knowledge of the Neotropical insect fauna.

70. *Zyginama bifida*, n. sp. (Figs. 4K, 71)
Description. Length of male 3.3 mm, female 3.3 mm. Ground color pale yellow; crown with pair of light brown preapical spots, apex with short median brown longitudinal stripe; mesepisternum, mesonotal triangles, and abdominal terga brown. Head (Fig. 4K) in dorsal view slightly wider than pronotum, crown longer medially than next to eye, anterior margin forming obtuse angle. Male pygofer (Fig. 71a) with dorsal appendage arising near base, elevated above dorsal margin of lobe, short, broad, apex bifid, with acute dorsal projection and rounded ventral lobe, not extended to apex of lobe; ventral appendage arising preapically, greatly elongate, twisted, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group vestigial. Aedeagus (Figs. 71b, c) with preatrium short; shaft compressed, in lateral view broad; subbasal processes absent; distal processes arising distad of gonopore, long, slender, curved ventrolaterad; apex bifid; gonopore arising near midlength of shaft.
Material examined. Holotype male, PERU, Madre de Dios, Rio Tambopata Res., 30 km (air) SW Pto. Maldonado, 290m, 12°50'S, 069°17'W, Smithsonian Institution Canopy Fogging Project, 10 November 1983, 03/02 (T.L. Erwin, et al.) [USNM]; 1 male paratype, same data [INHS]; 1 male paratype same data except 4 May 1984, 01/02/86 [USNM].
Notes. This species resembles *Z. adisi* in coloration but differs in having the crown shorter. It is unusual in lacking the ventrolateral setal group on the male pygofer. The species name refers to the bifid apex of the aedeagus.

71. *Zyginama truncata*, n. sp. (Figs. 4L, 72)
Description. Length of male 3.2 mm. Ground color pale yellow; crown unmarked; mesonotal triangles light brown; mesepisternum and abdominal terga light brown. Head (Fig. 4L) in dorsal view subequal in width to pronotum, crown longer medially than next to eye, anterior margin obtusely angulate. Male pygofer (Fig. 72a) with dorsal appendage arising near midlength, elevated above lobe, acuminate, nearly straight, ventral areolate, not extended to lobe apex; ventral appendage arising preapically, moderately long, extended dorsomesad; ventrolateral setal group with ~3 enlarged setae. Aedeagus (Fig. 72b, c) without preatrium; dorsal apodeme in lateral view slender; shaft compressed, in lateral view straight through most of length with basally angulate dorsal keel arising near midlength and extended to apex; subbasal processes absent; paired distal processes long,

slender, curved anterad; apex blunt, with pair of short triangular projections in posterior view; gonopore preapical on posterior surface.
Material examined. Holotype male, ECUADOR, Orellana, 1km S Onkonegare Camp, Reserva Etnica Waorani, 00°39'10"S, 076°26'00"W, 30 September 1996, fogging terra firme forest (T.L. Erwin, et al., lot#1696) [USNM].
Notes. This species closely resembles *Z. attenuata* but is easily distinguished by the distinctively broadened aedeagal apex. The species name refers to the truncate aedeagal apex.

72. *Zyginama ortha*, n. sp. (Figs. 4M, 73)
Description. Length of male 3.1 mm, female 3.1 mm. Ground color dull yellow; crown with very indistinct pair of brown submedial spots preapically; mesonotal triangles dark brown; meskatepisternum and abdominal terga brown. Head (Fig. 4M) in dorsal view subequal in length to pronotum, crown slightly longer medially than next to eye, anterior margin evenly rounded. Male pygofer (Fig. 73a) with dorsal appendage arising in basal half, elevated above and divergent from dorsal margin of lobe, nearly straight, acuminate, extended nearly to apex of lobe; ventral appendage arising at apex, long, extended posterodorsad; lobe between appendages rounded; ventrolateral setal group with ~4 enlarged setae. Aedeagus (Figs. 73b, c) without preatrium; dorsal apodeme in lateral view slightly broadened dorsally; shaft compressed, in lateral view moderately broad, nearly straight, without basal processes; paired distal processes arising adjacent to gonopore, slender, extended ventrad then curved anterodorsad; distal lobe compressed, bluntly rounded in lateral view.
Material examined. Holotype male, ECUADOR, Orellana, 1km S Onkonegare Camp, Reserva Etnica Waorani, 00°39'10"S, 076°26'00"W, 13 February 1999, fogging terra firme forest (T.L. Erwin, et al., lot#1032) [USNM]; 2 female paratypes, same data.
Notes. This species resembles *Z. attenuata* but differs in having paired spots on the crown, the dorsal pygofer appendage shorter, and the aedeagal shaft in lateral view broadest basad of the gonopore.

73. *Zyginama attenuata*, n. sp. (Figs. 4N, 74)
Description. Length of male 3.0 mm, female 3.2 mm. Ground color pale yellow, unmarked except indistinct tan mark at crown apex and dark brown mesonotal triangles. Head (Fig. 4N) in dorsal view subequal to pronotum in width, crown longer medially than next to eye, anterior margin forming obtuse angle. Male pygofer (Fig. 74a) with dorsal appendage arising in basal half, elevated above margin of lobe, attenuate, straight, extended nearly to apex of lobe; ventral appendage arising preapically, long, curved dorsomesad; lobe between appendages rounded; ventrolateral setal group with ~1 enlarged seta. Aedeagus (Figs. 74b, c) without preatrium, dorsal apodeme in lateral view weakly expanded dorsally; shaft strongly compressed, in lateral view nearly straight, gradually broadened toward apex; basal processes absent; distal paired processes arising distad of gonopore, long, slender, extended laterad and curved anterodorsad; apical lobe attenuate; gonopore preapical on posterior surface.
Material examined. Holotype male, PERU, Madre de Dios, Rio Tambopata Res., 30km (air) SW Pto. Maldonado, 290m, 12°50'S, 069°17'W, Smithsonian Institution Canopy Fogging Project, 8 November 1983 04/01/03 (T.L. Erwin, et al.) [USNM].
Notes. This species resembles several other South American Erythroneurini externally but is easily recognizable by the distinctive form of the aedeagus. The species name refers to the attenuate tip of the aedeagus.

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Appendix A. Morphological characters. Characters 1, 11, 12, 14, 15, 20, 23, 25, 26, 30, and 32 were treated as ordered (additive) in the phylogenetic analysis; others were treated as unordered.

1. Head in dorsal view with anterior margin: 0, broadly rounded; 1, obtusely angulate; 2, forming ca. 90° angle; 3, acutely produced.
2. Pygofer lobe dorsal margin: 0, convex; 1, concave
3. Pygofer dorsal appendage, origin: 0, in basal half of lobe; 1, in distal half of lobe.
4. Pygofer dorsal appendage, length: 0, > half length of lobe; 1, < half length of lobe.
5. Pygofer dorsal appendage, serrations: 0, absent; 1, present.
6. Pygofer dorsal appendage, shape: 0, slender, acuminate; 1, slender, blunt apically; 2, broad with acute apex; 3, truncate apically; 4, bifid; 5, with long, slender preapical spine; 6, with dorsal preapical angle.
7. Pygofer dorsal appendage, elevation: 0, not elevated above dorsal margin of lobe; 1, elevated above dorsal margin of lobe throughout length.
8. Pygofer dorsal appendage, curvature: 0, curved upward; 1, straight; 2, curved downward; 3, distinctly sinuate.
9. Pygofer ventral appendage: 0, absent, ventral margin of lobe weakly sclerotized; 1, present; 2, vestigial, ventral margin of lobe strongly sclerotized.
10. Pygofer ventral appendage, origin: 0, ventral, preapical; 1, at or near apex of lobe.
11. Pygofer ventral appendage, length: 0, > half length of lobe; 1, < half length of lobe; 2, very short, toothlike.
12. Ventrolateral setae: 0, absent; 1, 1-2 present; 2, 3-5 present; 3, 6 or more present.
13. Aedeagus ventrolateral flange: 0, absent; 1, present.
14. Aedeagal shaft width in lateral view: 0, very slender, no broader in lateral view than in posterior view; 1, broader in lateral view than in posterior view; 2, less than twice as long as broad; 3, as broad as long.
15. Aedeagal shaft shape in lateral view: 0, evenly recurved; 1, straight through most of length, posterior margin not concave preapically; 2, sinuate with posterior margin concave preapically.
16. Aedeagus apex in lateral view: 0, acuminate; 1, rounded; 2, broadly angulate; 3, falcate.
17. Aedeagus shaft apex: 0, not strongly recurved ventrad; 1, strongly recurved ventrad.
18. Aedeagus apex, posterior view: 0, slender, acuminate; 1, broad, rounded; 2, weakly emarginate; 3, deeply cleft.
19. Aedeagus dorsal retrorse preapical spine: 0, absent; 1, present.
20. Aedeagus paired basal processes, position relative to shaft: 0, posterad; 1, laterad through most of length.
21. Aedeagus posterior preapical spine: 0, absent; 1, present.
22. Aedeagus basal process(es): 0, absent; 1, present, paired; 2, present, unpaired.
23. Aedeagus paired distal processes: 0, absent; 1, present, even with or basad of gonopore; 2, present distad of gonopore.
24. Aedeagus paired distal processes, length: 0, short, triangular; 1, short, slender; 2, long, slender.
25. Aedeagus paired distal processes, orientation in lateral view: 0, extended anterad; 1, extended laterad; 2, extended posterad.
26. Aedeagus paired distal processes, orientation in posterior view: 0, ventrad; 1, ventrolaterad; 2, laterad; 3, dorsad.
27. Aedeagus paired distal processes: 0, unbranched; 1, branched.
28. Aedeagus paired teeth or keels near midlength of shaft: 0, absent; 1, present.
29. Aedeagus anterior hump near midlength of shaft: 0, absent; 1, present.
30. Aedeagus preatrium: 0, very short; 1, well developed but distinctly shorter than shaft; 2, subequal to or longer than shaft.
31. Aedeagus dorsal apodeme: 0, slender; 1, broad.
32. Gonopore: 0, apical; 1, preapical on posterior surface; 2, at or basad of midlength.
33. Head: 0, without small black apical spot; 1, with small black apical spot.

34. Face: 0, without transverse brown band dorsallly; 1, with transverse brown dorsal band.
35. Face (color): 0, more or less uniformly pale or brown; 1, with distinct transition between dark ventral section and pale dorsal margin.
36. Crown (paired dark spots): 0, without pair of dark brown preapical spots; 1, with pair of dark brown preapical spots.
37. Crown (oranage maculae): 0, without orange maculae; 1, with pair of orange maculae; 2, with median orange macula.
38. Scutellum apex: 0, not black; 1, black, contrasting with pale anterior region.
39. Forewing color pattern: 0, markings indistinct or absent; 1, with oblique longitudinal yellow or orange stripes; 2, with symmetrically arranged brown or reddish patches; 3, with transverse bands.
40. Pronotum: 0, with pair of triangular orange spots; 1, with pair of curved orange submedial stripes; 2, with median V- or U-shaped mark; 3, anterior two-thirds red with white anterolateral spots; 4, with median posterior orange area, anterolateral border white; 5, without distinct markings.

Appendix B. Data matrix for phylogenetic analysis. Character codes correspond to descriptions in Appendix A. Question marks indicate that the character is missing or inapplicable for the corresponding taxon.

	1111111111222222222333333333
Taxon/Character	1234567890123456789012345678901234567890
Z. agnata	20000102112201010001011202000010000050 1
Z. arizonica	20000102111301120001112210010111000001 01
Z. aucta	20110212101300110 20?020????0000100001001
Z. blanda	20000202101301010 1?00220110010100000?01
Z. casta	20000001111201010000012210000001100011 01
Z. cimmaroni	2000000011120110000?00220200011100001?01
Z. cornigera	200000022??200010101012201100001000010 01
Z. erosa	20000002111200010000011201100001000010 12
Z. grandis	11010002101301000001010????0000100101302
Z. iguala	20000202101301010000111220000001000 02?03
Z. inornata	20110602101102200 0?10120300111100010?00
Z. merita	20110212111300110 20?020??0101100001001
Z. munda	2011020110020 10?0001010????0011100002400
Z. nicholi	21010002101201100000011002000001001013 03
Z. novella	20110103111101120 00?022002000110000110 1
Z. nuda	20000103110101010 00?0022??0001120000 0?00
Z. obscura	20000003111200110000011001000001000005 00
Z. pallenta	20100001100201000 0?0010020001010000 1?01
Z. pinalensis	20110202101202200 0?1011020011110000 1101
Z. ritana	20100002101302010101010????0010100000401
Z. rubicunda	11010002101201100000011002000001000013 02
Z. sola	20000502101300010000011102000001000 1?02
Z. spectabilis	21010601101301100000010????0000100101303
Z. triceroprocta	10010001112300000 0?0012031000010000 1?01
Z. tricolor	30010001100200210 0?100????0000101000402
Z. tripunctata	20000002111200010000010????0000110010?11
Z. unicolor	20000402101200010000011 20?00010100000500
Z. utahna	20?10602111101000 0?1012010000110000 1?01
Z. angulata	20010202112200 0?0?0001120210000100101111
Z. brunnedorsum	30100003111202200 0?1012010011110000 0?02
Z. carapana	20100202101200010001010????0011100000411
Z. coahuilensis	20000001111201010001012 1??00000110010111
Z. colima	20100502102300010 00?000????1000110000012
Z. colorada	10100003111101100 0?1012210001110000 1?01
Z. cuernavaca	20000201101300010000010????0000110000012
Z. durangensis	20000002101201110000011202010001000011 01
Z. elongata	20010201111201110000012210000001100 0?11
Z. enigmata	20100103101102210000011101001111000 1?11
Z. lanceolata	21110000111200100 0?100????0000100000502
Z. maculipennis	20010202101000200000010????0011100000110

Appendix B continued.

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                          1111111111222222222233333333334
Taxon/Character   12345678901234567890123456789012345678890
-----------------------------------------------------------
Z. malleta        ?000010210120112000101O????10001?????11
Z. multifurca     200104011013000003O?00220110000110010?1?
Z. ochrescens     201101121112000101O?00121000000100000502
Z. olmeca         210000121122010200O?00120100000101002202
Z. orizaba        200000021112000000010110020000011000O?10
Z. pallescens     200102021011011?030?00121100001100001?12
Z. panamensis     100100021012001100l?100????000110000O?12
Z. queretarensis  200101021012011100010112100100011001O?12
Z. rodmani        200000011122011100000l0????000011001l?12
Z. rossi          210100011013011000000112100000010011l302
Z. rubrocta       200000021003001200O?021200000001000O2?03
Z. serrata        100013101010121100O?00120200010210000?00
Z. spatulata      200001031011011200O?00110200011100001?01
Z. tolteca        200000111000000100O?000????0010100101212
Z. toluca         200000111113011103O?00220210100110010?11
Z. vittata        200100021111001103O?00120?1001110000l?01
Z. zitacuarensis  200000021112011200010l0????1000100001111
Z. adisi          100002011013000100O?0010?200010000010500
Z. attenuata      100000111011011000O?00220100000110000500
Z. bifida         100104111000010103O?00221100001100010500
Z. cristata       100000121012000100O?00120100000100000500
Z. elevata        001100121002001?031?00121?10000000000500
Z. furca          100004111013131?0?0?000????0001?00000500
Z. gibba          201102101113000100O?00220100000200000500
Z. gracilifurca   101000001002000000O?00120110000110010500
Z. intermedia     201100121113010100O?00120110000110000500
Z. longispina     000000111003101?100?00220?00000200010500
Z. ortha          100000111102011100O?00120100000110010500
Z. spiculata      100013121013131203?0?000????0000?00000500
Z. tambopatensis  101104121003111?100?00222??0000200010500
Z. truncata       100000121012011103O?00121100000100000500
Mexigina oculata  20??????000202010303?001?120000010002O?0?
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Species Index

(junior synonyms in *italics;* pages of individual species accounts in **bold**)

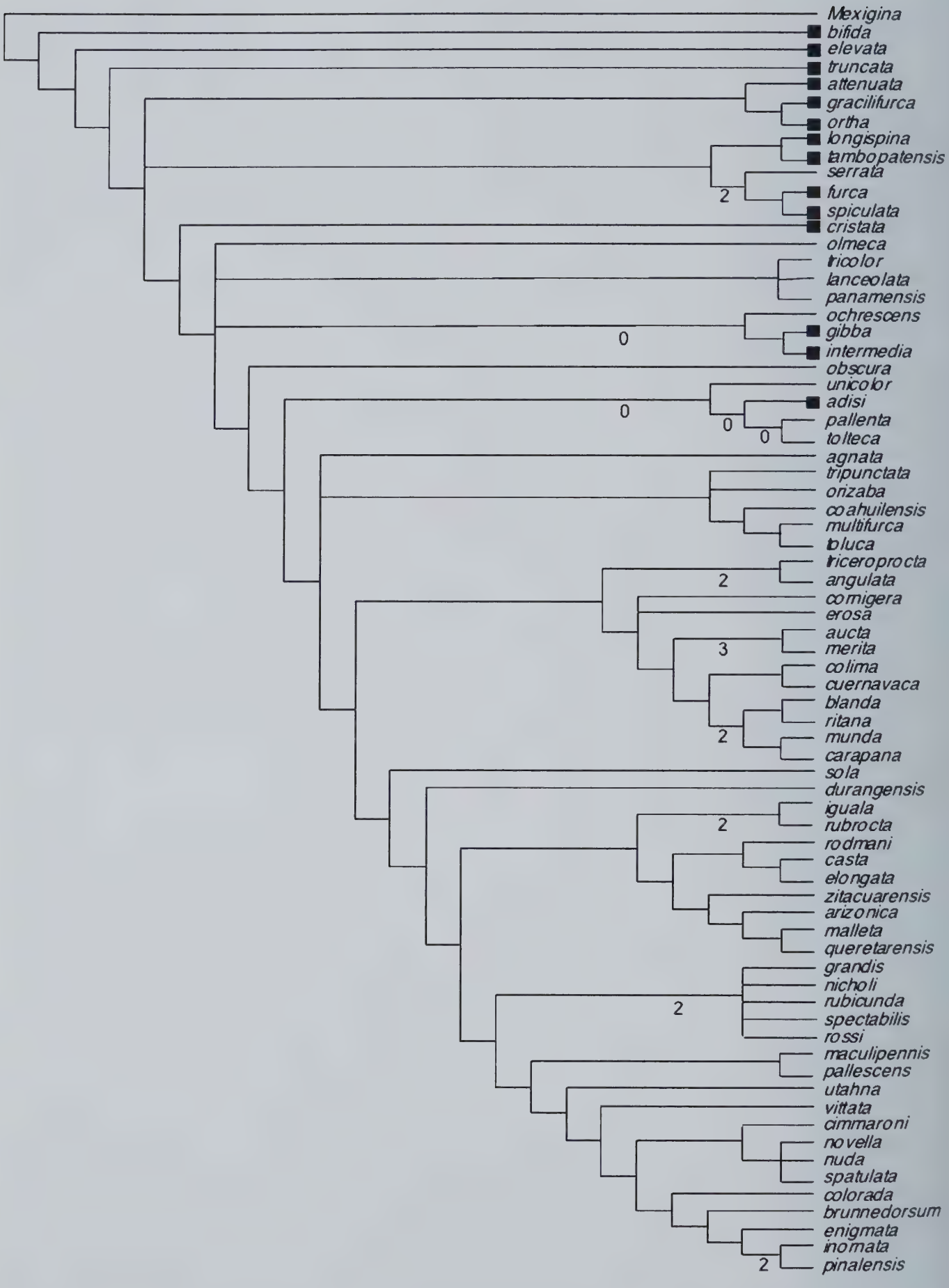


Figure 1. Adams consensus of 1,270 equally parsimonious trees from analysis of data matrix in Appendix B. All consistently resolved nodes had decay index = 1 except as indicated. Nodes with decay index = 0 collapsed in the strict consensus. Black squares indicate endemic South American species.

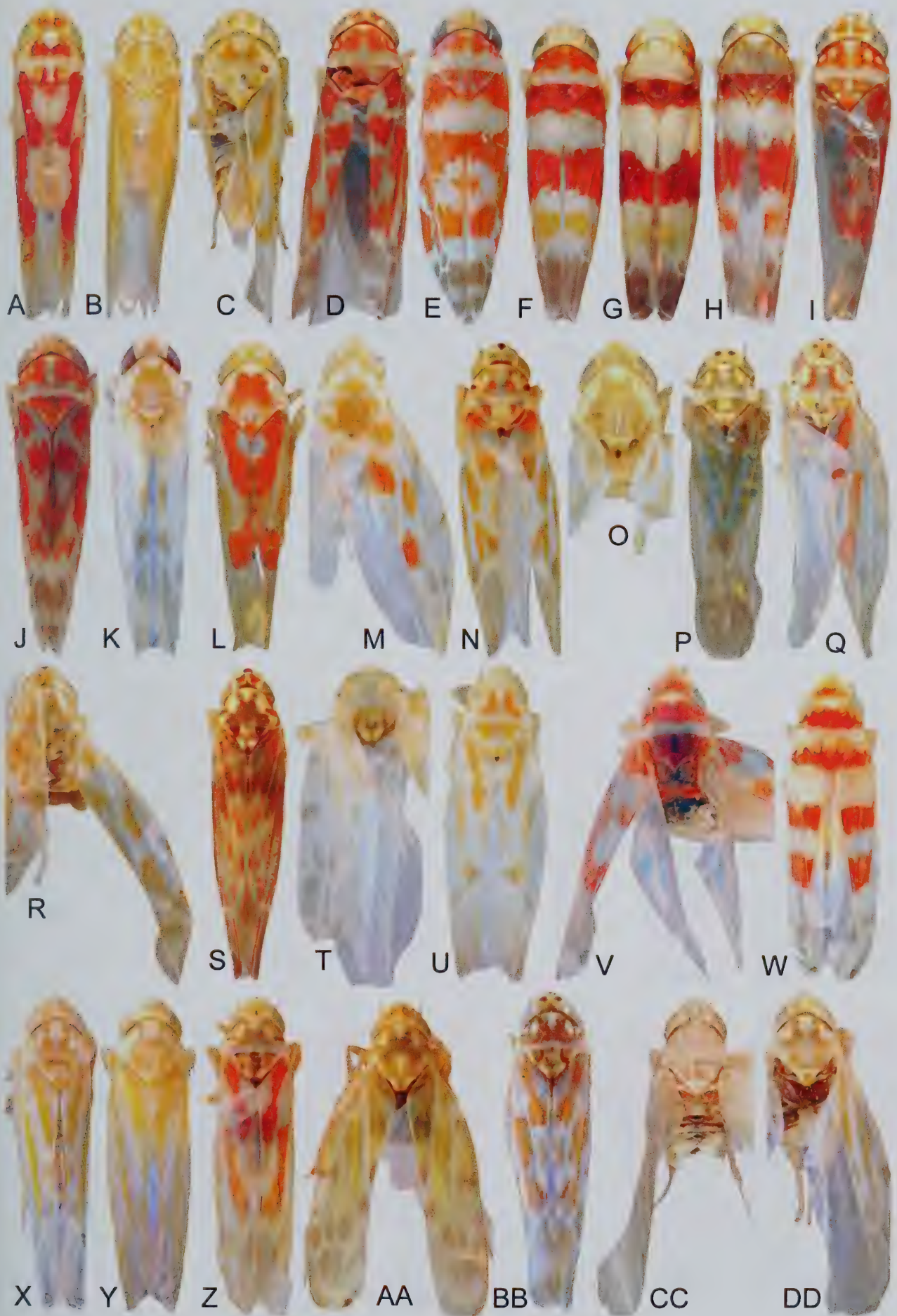


Figure 2. *Zyginama* spp., dorsal habitus of North American species (not to scale). A, *Z. aucta*; B, *Z. merita*; C, *Z. dentata* (lectotype female); D, *Z. grandis*; E, *Z. spectabilis*; F, *Z. nicholi* (holotype); G, *Z. nicholi* (female paratype of *Z. ales*); H, *Z. nicholi* (male paratype of *Z. canyonensis*); I, *Z. rubicunda* (holoype female); J, *Z. rossi*; K, *Z. munda*; L, *Z. ritana*; M, *Z. maculipennis*; N, *Z. cuernavaca*; O, *Z. carapana*; P, *Z. tripunctata*; Q, *Z. coahuilensis*; R, *Z. orizaba*; S, *Z. rodmani*; T, *Z. malleta*; U, *Z. zitacuarensis* V, *Z. rubrocta*; W, *Z. iguala*; X, *Z. novella*; Y, *Z. arizonica*; Z, *Z. elongata*; AA, *Z. enigmata*; BB, *Z. queretarensis*; CC, *Z. obscura* (holotype male); DD, *Z. angulata*.

Figure 3. *Zyginama* spp., dorsal habitus of new North American species (not to scale). A, *Z. durangensis*; B, *Z. unicolor* (holotype male); C, *Z. sola*; D, *Z. cornigera*; E, *Z. erosa*; F, *Z. casta*; G, *Z. agnata*; H, *Z. panamensis*; I, *Z. colima*; J, *Z. lanceolata*; K, *Z. tricolor*; L, *Z. tolteca*; M, *Z. nuda*; N, *Z. brunnedorsum*; O, *Z. pinalensis* (holotype male); P, *Z. triceroprocta* (holotype); Q, *Z. multifurca*; R, *Z. colorada*; S, *Z. vittata*; T, *Z. cimmaroni*; U, *Z. inornata*; V, *Z. utahna* (holotype male); W, *Z. serrata*; X, *Z. spatulata*; Y, *Z. ochrescens*; Z, *Z. toluca*; AA, *Z. pallescens*; BB, *Z. blanda*; CC, *Z. pallenta* (holotype male); DD, *Z. olmeca*; EE, *Z. ternaria* (holotype female).

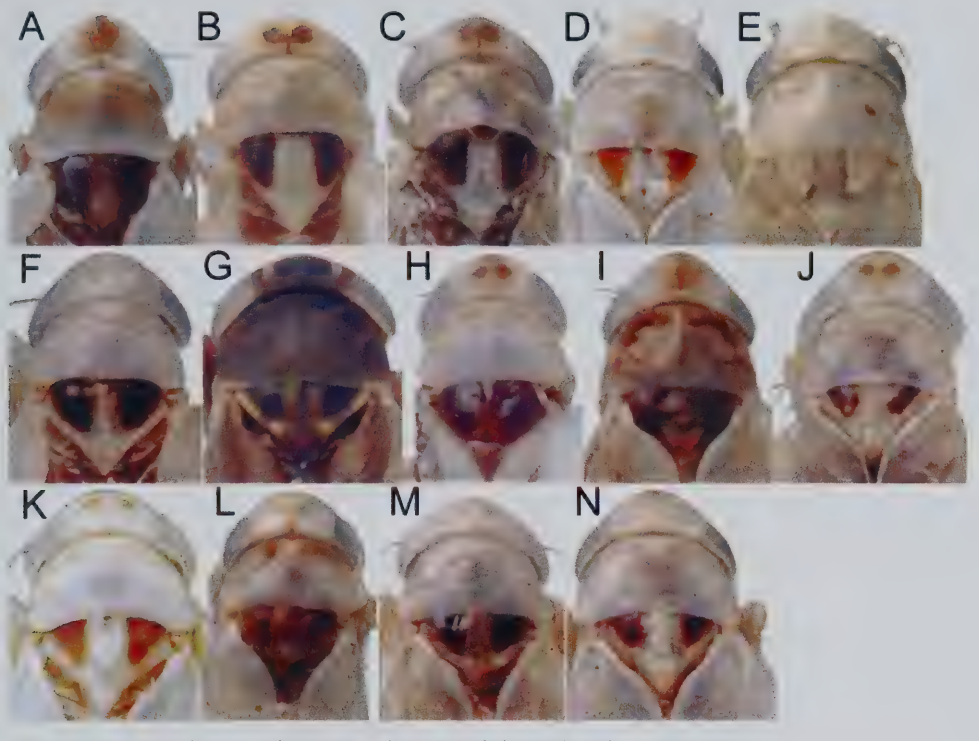
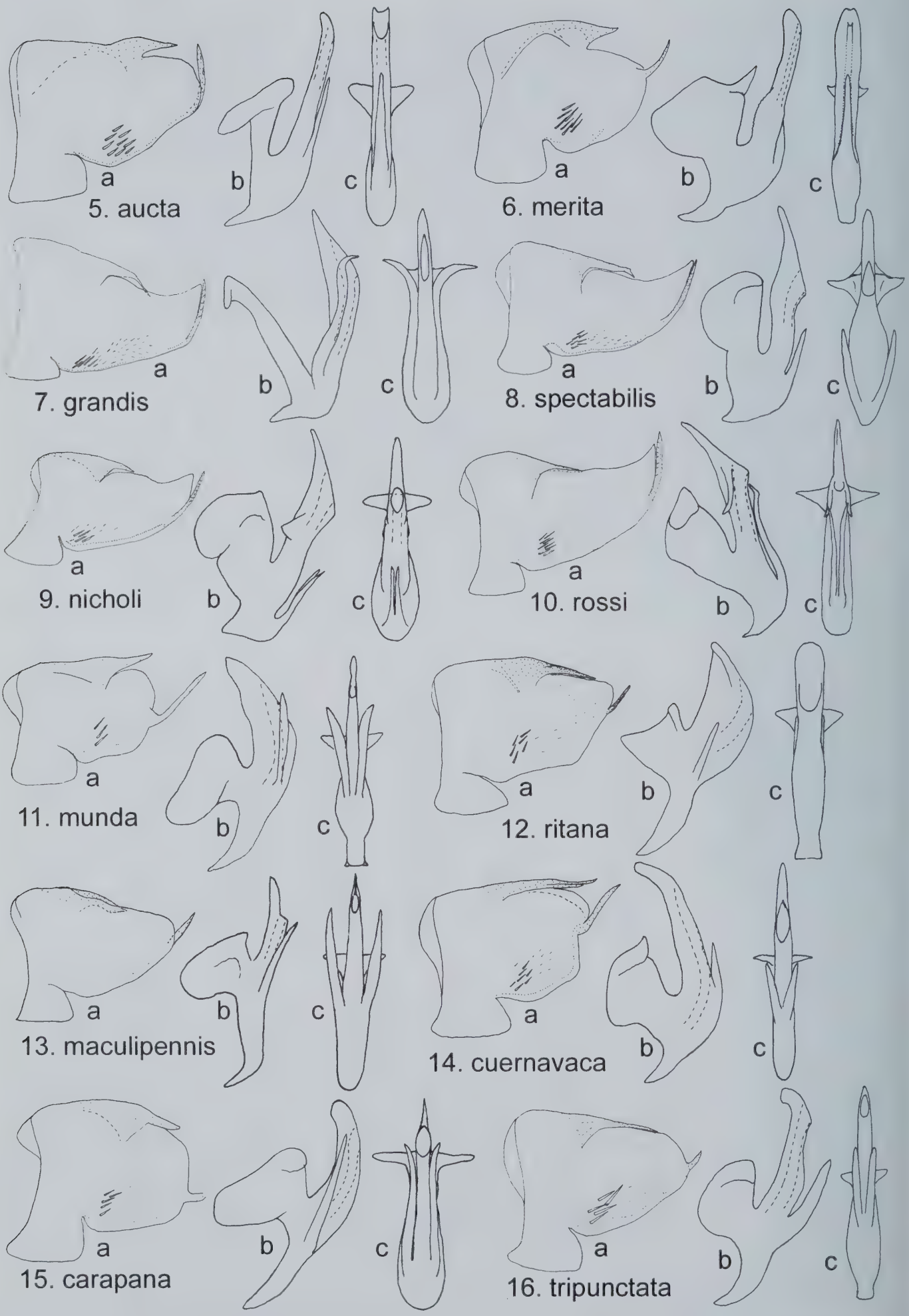
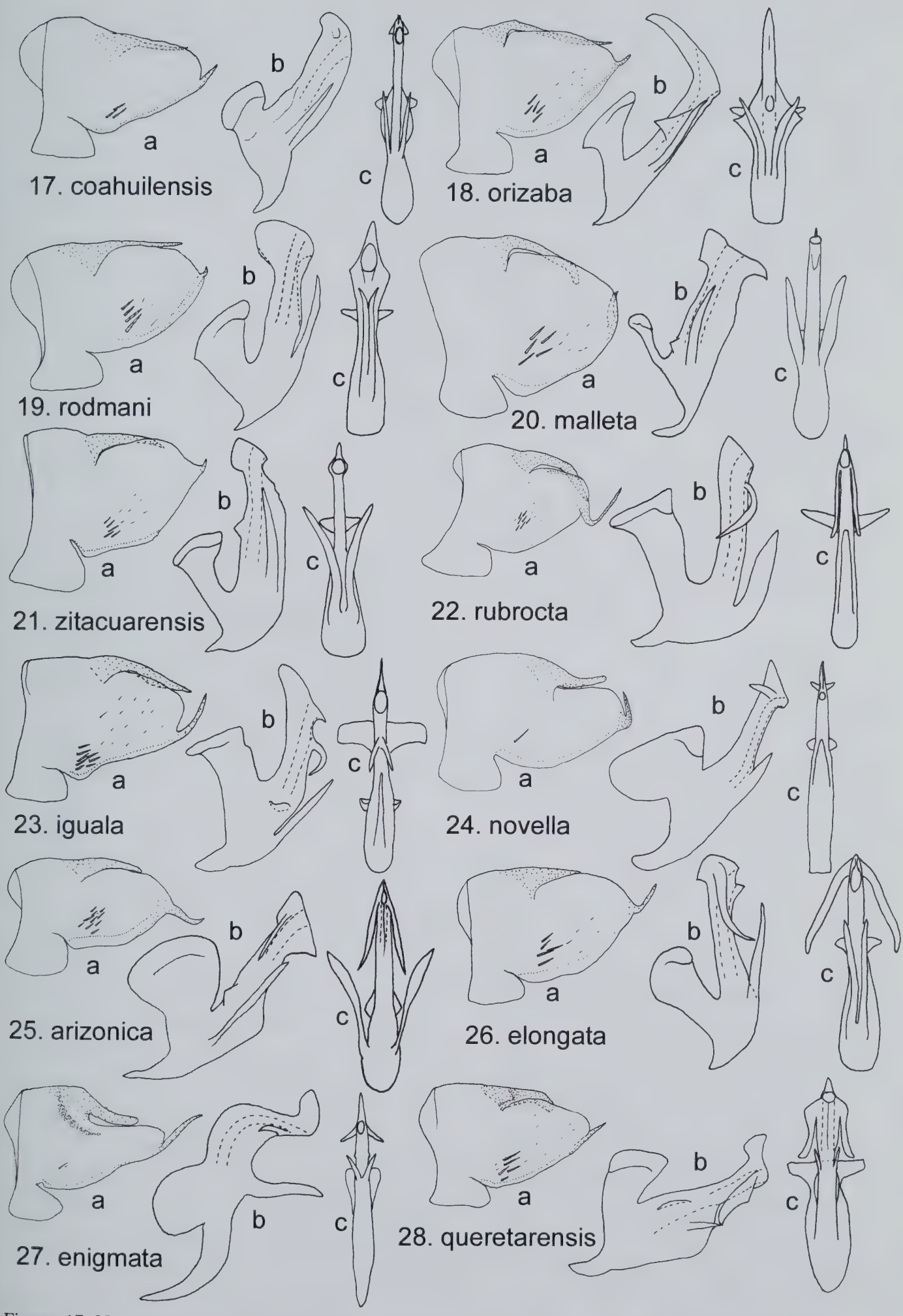


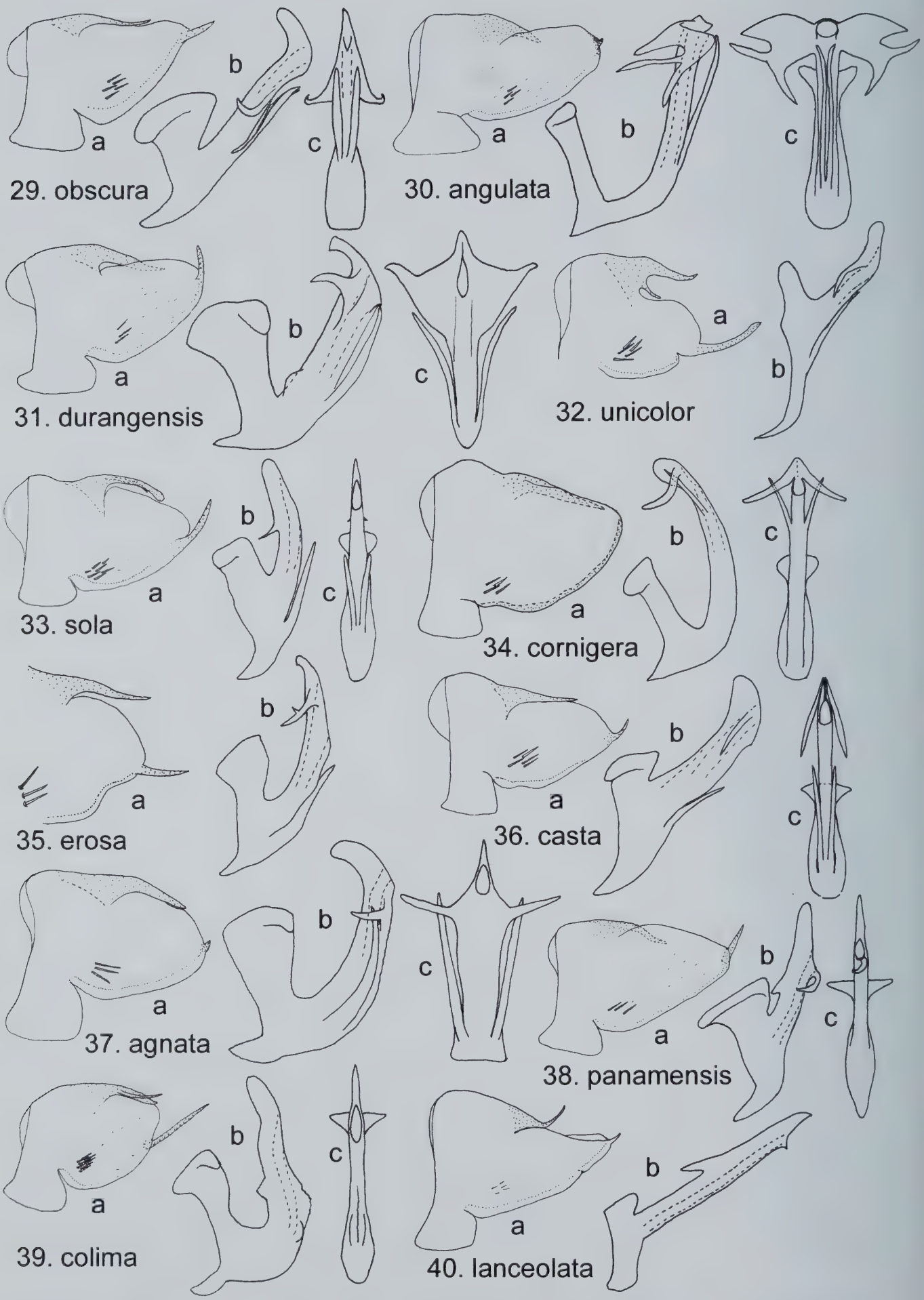
Figure 4. South American species provisionally placed in *Zyginama*, dorsum of head and thorax (not to scale). A, *Z. gibba*; B, *Z. longispina*; C, *Z. tambopatensis*; D, *Z. furca*; E, *Z. spiculata*; F, *Z. cristata*; G, *Z. elevata*; H, *Z. gracilifurca*; I, *Z. intermedia*; J, *Z. adisi*; K, *Z. bifida*; L, *Z. truncata*; M, *Z. ortha*; N, *Z. attenuata*.



Figures 5–16. *Zyginama* spp., male genitalia: a, pygofer, lateral view; b, aedeagus, lateral view; c, aedeagus, posterior or posteroventral view.



Figures 17–28. *Zyginama* spp., male genitalia: a, pygofer, lateral view; b, aedeagus, lateral view; c, aedeagus, posterior or posteroventral view.



Figures 29–40. *Zyginama* spp., male genitalia: a, pygofer, lateral view; b, aedeagus, lateral view; c, aedeagus, posterior or posteroventral view.

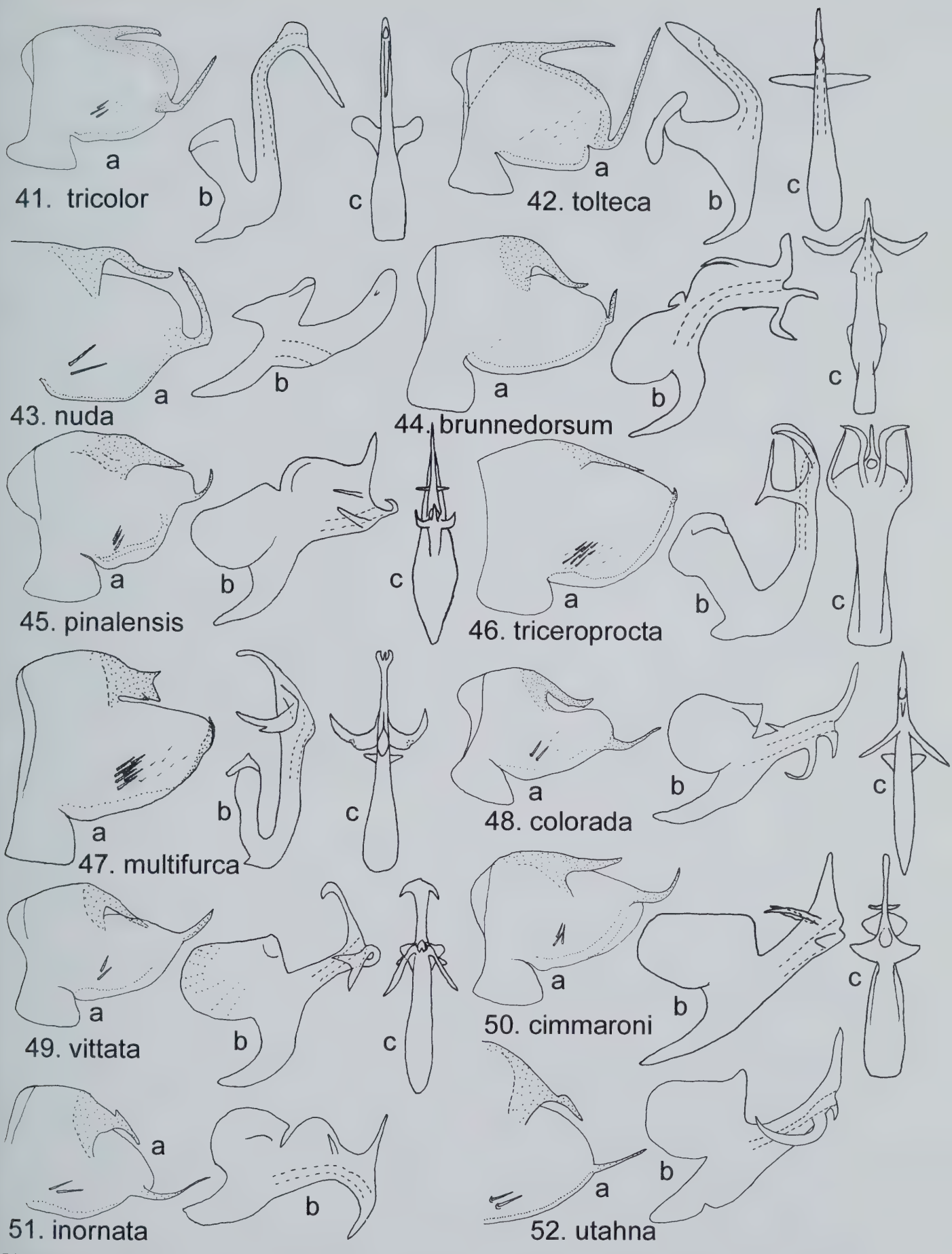


Figure 41–52. *Zyginama* spp., male genitalia: a, pygofer, lateral view; b, aedeagus, lateral view; c, aedeagus, posterior or posteroventral view.

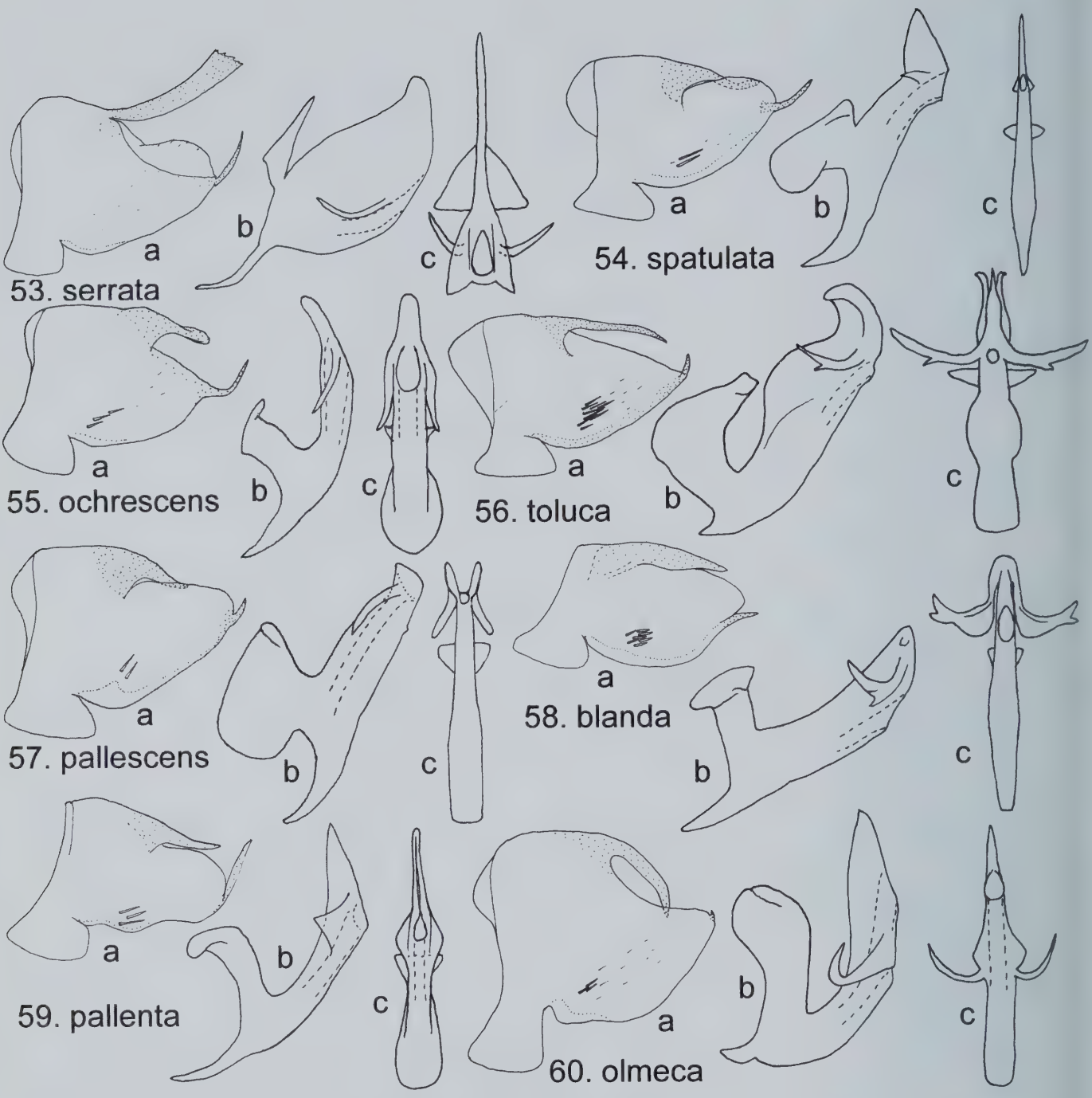
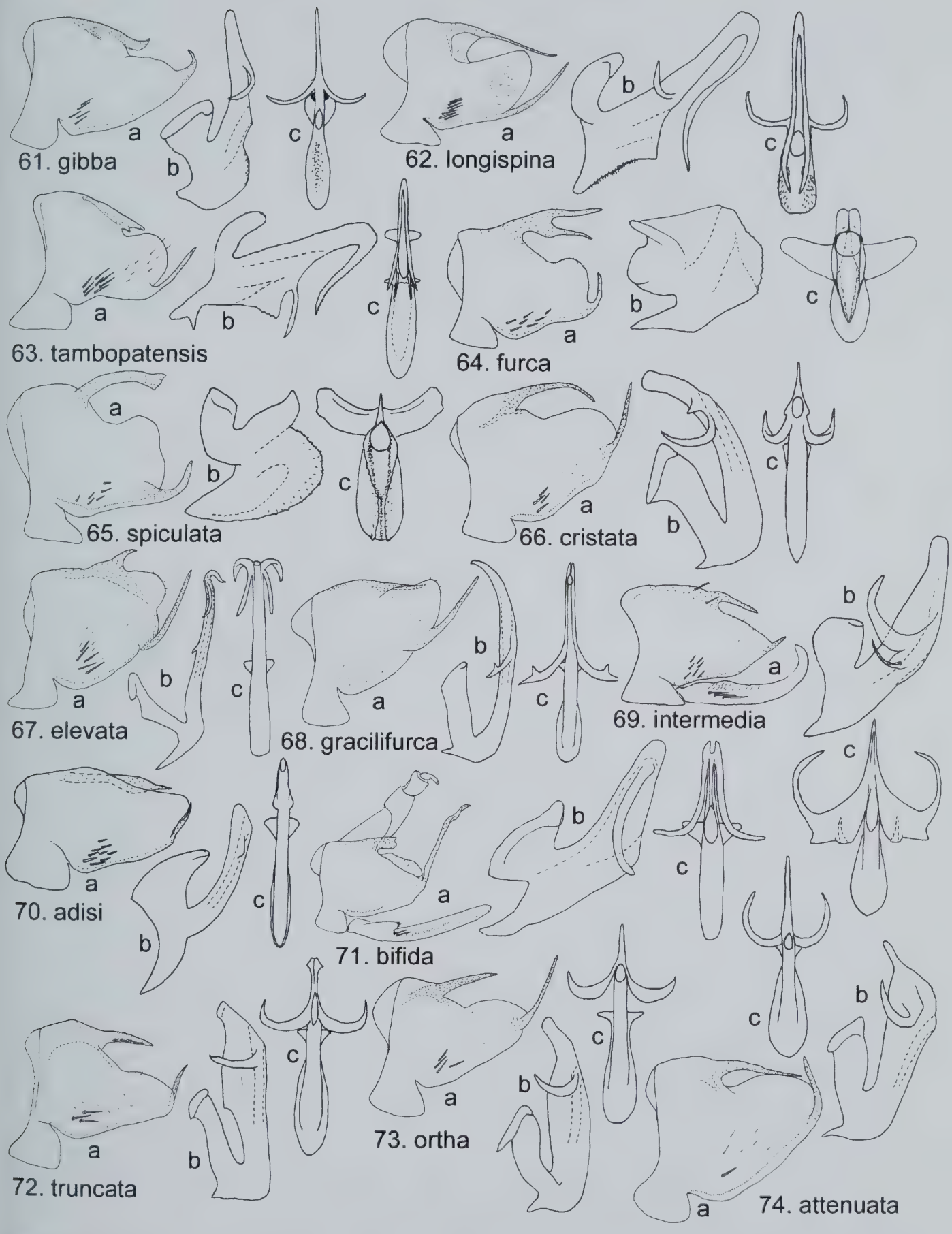


Figure 53–60. *Zyginama* spp., male genitalia: a, pygofer, lateral view; b, aedeagus, lateral view; c, aedeagus, posterior or posteroventral view.



Figures 61–74. South American species provisionally placed in *Zyginama*, male genitalia: a, pygofer, lateral view (except 69a, pygofer and subgenital plate; 71a, entire genital capsule); b, aedeagus, lateral view; c, aedeagus, posterior or posteroventral view.

Notes

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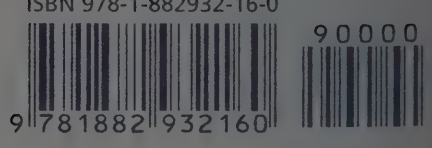
A Division of the Illinois Department of Natural Resources

ISBN 978-1-882932-16-0



ILLINOIS
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Vascular Flora of Middle Fork Woods Nature Preserve, Vermilion County, Illinois

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Illinois Natural History Survey Bulletin
Volume 38, Article 4
June 2008

Illinois Natural History Survey, Brian Anderson, Chief
A Division of the Illinois Department of Natural Resources

Illinois Natural History Survey
Distribution Office
I-Building
1816 South Oak Street
Champaign, IL 61820

Citation:
Larimore, R.L., L.R. Phillippe, and J.E. Ebinger. 2008. Vascular Flora of Middle Fork Woods Nature Preserve, Vermilion County, Illinois. Illinois Natural History Survey Bulletin 38(4):177–196.

Editor: Charles Warwick

US ISSN 0073-4918

US ISBN 1-882932-17-X

Printed by authority of the State of Illinois

P0182869—.75M—06-08

Printed with soy ink on recycled and recyclable paper.

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Contents

ACKNOWLEDGMENTS

The authors would like to thank the Illinois Nature Preserves Commission and the Illinois Department of Natural Resources for permission to study the preserve. Thanks are also given to: Dave Ketzner, Tim Whitfeld, Rachel Larimore, Jeff Matthews, Mary Cooprider, and Rob Hackett for help in collecting the voucher specimens, and Brad Zercher for help with GPS/GIS. Thanks to Dave Ketzner, Connie Carroll-Cunningham, Paul Tessene, and Bill McClain for reviewing this manuscript. This study was supported by the Illinois Department of Transportation, and a grant from the Illinois Wildlife Preservation Fund.

ABSTRACT
The vascular flora of Middle Fork Woods Nature Preserve, Vermilion County, Illinois, was studied during the growing seasons of 1999–2002. A total of 376 species were found: 12 ferns, fern-allies, and gymnosperms; 99 monocots; and 265 dicots. The three families with the largest number of species were the Poaceae (44), Asteraceae (39), and Cyperaceae (34, 29 of which were members of the genus *Carex*). The overstory and woody understory of six forest communities were surveyed: a mature second growth dry-mesic upland forest dominated by *Quercus alba* (white oak) and *Q. velutina* (black oak); an old growth, dry-mesic savanna dominated by *Q. alba* with a dense understory of *Acer saccharum* (sugar maple); SW-facing and NE-facing forested slopes of a mesic ravine, both dominated by *A. saccharum* and *Q. alba*; a southern flatwood forest/ephemeral pond community dominated by *Q. bicolor* (swamp white oak); and an immature second growth dry-mesic upland forest dominated by *Q. alba* and *Carya ovata* (shagbark hickory). Ground layer plants were surveyed in spring and fall in the dry-mesic upland forest communities, and for each species the relative cover, relative frequency, and importance values were determined. The preserve, comprised mostly of oak-hickory forest communities, was found to be in relatively good ecological condition. Mature and maturing second-growth oaks were present throughout much of the preserve. Sugar maples dominated the understory and, along with the dense overstory, were apparently limiting oak regeneration. The non-natives *Lonicera* spp. (bush honeysuckles), *Elaeagnus umbellata* (autumn olive), *Alliaria petiolata* (garlic mustard), and the native sugar maple, will continue to need to be controlled. Prescribed fire is recommended to limit populations of these species.

INTRODUCTION

The 32.4-ha Middle Fork Woods Nature Preserve (MFWNP) is located in central Vermilion County, along the eastern border of central Illinois, within the 1,153-ha Kickapoo State Park. The Middle Fork of the Vermilion River, about 27 km of which is designated as a National Scenic River, runs through the park. Approximately 2 km north of MFWNP, on the west side of the river, is the Middle Fork State Fish and Wildlife Area, encompassing 1,700 ha. North of Kickapoo Park and east of the river is the 1,214- ha Kennekuk Cove County Park. The Middle Fork of the Vermilion River forms the preserve boundary on the east, with old strip-mine land and lakes beyond the river. The land north of the preserve is logged and grazed upland forest and to the west a small creek forms the boundary, along with a county road and privately owned woods. An old-field of early successional native forest species that contains an abundance of exotic plant species lies to the south. This old-field was used as a base camp for the Civilian Conservation Corps (CCC) from 1939 to 1942 (McClain 1984, Wallace 1975).

The forest communities of MFWNP were previously studied (Wallace 1975), but the results of this investigation were not published. The MFWNP is one of nine dedicated nature preserves in Vermilion County. Of these preserves, the vegetation of only a few has been studied. Larimore et al. (1999) examined the forests at Horseshoe Bottom Nature Preserve, while Ebinger (1981) studied the glacial drift hill prairie at Windfall Prairie Nature Preserve. Though not a dedicated nature preserve, the vegetation of the Vermilion River Observatory was recently examined (Phillippe et al. 2003).

Much of the land surface within Kickapoo State Park was strip-mined and the park is currently composed of strip-mine lakes and mounds of mine spoils now covered with an abundance of successional vegetation and numerous invasive exotic species. During the strip mining operations MFWNP was not mined. Before being dedicated as a nature preserve in 1979, the area was subjected to disturbances, particularly selective timber cutting in the early 1900s, and was probably grazed until 1939 (McClain 1984). Presently the forests are recovering and the MFWNP has a high diversity of plant and animal life. The present study was undertaken to document the vascular flora of the preserve and to determine the composition and structure of the forest communities present.

DESCRIPTION OF THE STUDY AREA

Situated within the Vermilion River Section of the Wabash Border Natural Division, the MFWNP is on the Wisconsin Till Plain about 80 km north of the terminal moraine of Wisconsin glaciation (Schwegman et al. 1973). This level region, exposed by the retreating Wisconsinan glaciation, was dissected by rapid down-cutting by post-glacial rivers, resulting in the presently entrenched Middle Fork of the Vermilion River. This area is presently characterized by rugged topography along major streams that are surrounded by relatively flat uplands. Pre-settlement vegetation was mostly wet-mesic to dry forests in ravines and on the dissected uplands, with mesic prairie, savanna, and open woodlands on flat to gently rolling uplands (Anderson 1991, Ebinger and McClain 1991).

The area now known as MFWNP was in private ownership from the early 1800s to the late 1930s (Wallace 1975). Between 1910 and 1915 the United Electric Coal Company purchased large tracts of forest along the west bank of the Middle Fork of the Vermilion River including all of the land now comprising MFWNP, and logged parts of the uplands for mine timbers. In 1939 the State of Illinois purchased the land from the United Electric Coal Company and started developing the site into Kickapoo State Park. Since 1942 the area that became the MFWNP has been relatively undisturbed though a few paths were developed, and a picnic area was maintained where the savanna community presently exists (Fig. 1). When MFWNP was dedicated in 1979, the trails and the picnic area were abandoned (McFall and Karnes 1995). A loop trail through the preserve was being maintained at the time of our study.

This 28-ha preserve, with an additional 4.4 ha of buffer, is located approximately 7.7 km west of Danville, Illinois (SE1/4 Sec 32, T20N R12W and N1/2 Sec 5, T19N R12W). The elevation varies from 167.6 m above sea level at the river to 195.0 m in the uplands. The climate of east-central Illinois is continental with cool winters, hot summers, and little or no water deficit in any season of the year (Page 1949, Fehrenbacher et al. 1967, Schwegman et

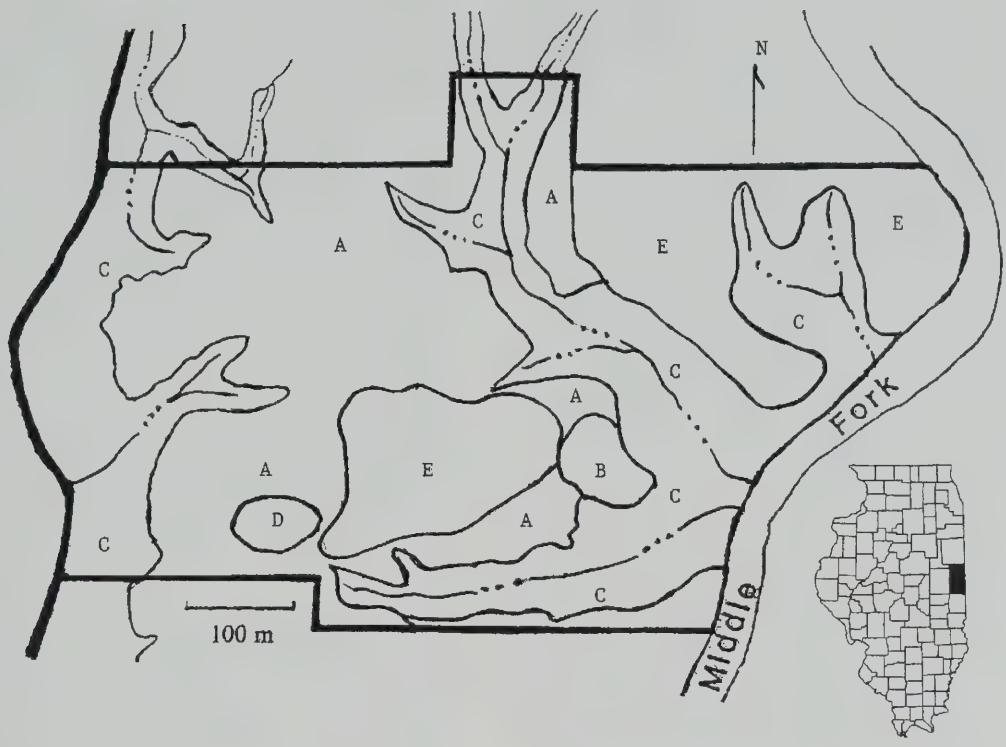

Figure 1. Forest communities within Middle Fork Woods Nature Preserve, Vermilion County, Illinois. (A) mature second growth dry-mesic upland forest, (B) old growth dry-mesic savanna, (C) mesic ravine upland forest, (D) southern flatwood forest/ephemeral pond, and (E) immature second growth dry-mesic upland forest.

al. 1973). In Danville, Illinois, average annual precipitation is 102.0 cm, with the month of July having the highest rainfall with a mean average of 11.3 cm, and January and February being the driest months, each averaging 4.8 cm of precipitation. Mean average annual temperature in Danville is 11.3° C, with the hottest month being July with a mean average of 24° C and the coldest being January with a mean average of -3.8° C. The number of frost-free days varies from 170 to 180 (Midwestern Regional Climate Center 2004).

The silvery salamander (*Ambystoma platineum*), a state endangered species, is found in the preserve (Herkert 1992). This unisexual polyploid species is known from scattered sites in the eastern United States. At the MFWNP the salamander uses the ephemeral ponds in a southern flatwoods community for reproduction (Morris 1974). An additional pond has been constructed in the buffer area of the preserve to ensure an adequate water supply for this species (Herkert 1992, Mui 2004).

Further information on this study, including GPS coordinates, can be found in the Illinois Nature Preserves Commission/Natural Area files at the Illinois Natural History Survey (INHS) Library in Champaign.

MATERIALS AND METHODS

Vascular species present: During the growing seasons of 1999, 2000, and 2001, the vascular flora of MFWNP was surveyed. Voucher specimens were collected, habitats for each species determined, and the plant communities delineated. Specimens collected were identified and deposited in the herbarium of the Illinois Natural History Survey, Champaign, Illinois (ILLS). The criteria for designating non-native taxa followed Gleason and Cronquist (1991) and Mohlenbrock (2002), whereas nomenclature follows Mohlenbrock (2002). The classification of forest community types mostly followed that of White and Madany (1978).

Overstory survey: In 2000 the overstory of the mature second growth dry-mesic upland forest at MFWNP was sampled using 0.03-ha circular plots. These plots were established at 30 m intervals along two north/south transects

(50 plots total). In each plot all living and dead-standing individuals ≥10.0 cm dbh were identified and their diameters recorded (Tables 1 and 2). From this data, living-stem density (stems/ha), basal area (m^2/ha), relative density, relative dominance (basal area), importance value (IV), and average diameter (cm) were calculated for each species. Determination of the IV follows the procedure used by McIntosh (1957) and is the sum of the relative density and relative dominance. Density (stems/ha), basal area (m^2/ha), and average diameter (cm) were determined for dead-standing individuals.

The remaining communities were much smaller and were surveyed by dividing the majority of the area of each community into contiguous quadrats 25 m on a side, the number of quadrats being determined by the size of each area. These included: 4 quadrats in an old growth dry-mesic savanna (Table 3); 8 quadrats in a SW-facing mesic ravine forest (Table 4); 8 quadrats in a NE-facing mesic ravine forest (Table 5); 4 quadrats in a southern flatwoods forest/ephemeral pond community (Table 6), and 16 quadrats in a second growth immature dry-mesic upland forest (Table 7). The data were collected and analyzed in the same way as those for the mature second growth forest.

Woody understory survey: The woody understory composition and density (stems/ha) were determined for each forest community using nested circular plots 0.0001, 0.001, and 0.01 ha in size located at 15-meter intervals along randomly located transects within each community. Four additional 0.0001-ha circular plots were located 7 m from the center points of each plot center along cardinal compass directions. Counts were recorded of woody seedlings and shrubs (≤ 50 cm tall) in the 0.0001-ha plots, of small saplings and shrubs (> 50 cm tall and < 2.5 cm dbh) in the 0.001-ha plots, and of large saplings and shrubs (2.5–9.9 cm dbh) in the 0.01-ha plots.

Ground layer survey: The ground layers in the dry-mesic upland forest communities were surveyed in the late summer of 2001 (Tables 8 and 9) and late spring of 2002. In each community a 50 m line transect was randomly located and the ends marked with steel stakes. Along each transect 1 m^2 quadrats were spaced at 1 m intervals (n=50/transect), odd-numbered quadrats to the right, even-numbered to the left. A random numbers table was used to determine the number of meters (0 to 9) the quadrat was located from the transect line. Species cover was determined using the Daubenmire cover class system (Daubenmire 1959) as modified by Bailey and Poulton (1968). Importance value (IV) for ground layer species was determined by summing relative cover and relative frequency.

RESULTS

Vascular flora: The vascular flora of MFWNP consisted of 376 species within 231 genera and 92 families. Of these species, 40 (10.6%) were not native to Illinois. Ferns, fern-allies, and gymnosperms were poorly represented at MFWNP, accounting for only 12 species (3%), whereas angiosperms accounted for the remainder. Among the angiosperms, monocots accounted for 99 species (26%) in 44 genera and 11 families, while dicots accounted for 265 species (71%) in 181 genera and 73 families. Families with the most species were: Poaceae (44 species), Asteraceae (39), Cyperaceae (34), Rosaceae (16), Brassicaceae (12), Lamiaceae (11), Apiaceae (11), Ranunculaceae (10), and Scrophulariaceae (10). These taxa are listed in Appendix I.

Mature second growth dry-mesic upland forest: Covering most of the western half of MFWNP, this community was dominated by *Quercus alba* (white oak), which accounted for more than one-third of the overstory trees (138.5 stems/ha), half of the total basal area (16.762 m^2/ha), and nearly half of the IV (90 out of 200). *Quercus velutina* (black oak) ranked second with an IV of 33.3, and *Acer saccharum* (sugar maple) was third with an IV of 22.5 (Table 1). The oaks dominated the larger diameter classes as suggested by their average diameters of 37.3 cm dbh and 42.9 cm dbh, respectively. *Acer saccharum*, in contrast, was common in the smaller diameter classes as indicated by an average dbh of 15.0 cm. *Acer saccharum* was also common in the seedling and sapling categories. Dead-standing individuals averaged 43.5 stems/ha with the oaks being well represented (Table 2). A total of 33 woody species were encountered in this community (Table 1).

The woody understory of the upland forest was dominated by numerous small seedlings of

Fraxinus americana (white ash) along with the shrubs *Lindera benzoin* (spicebush) and *Viburnum prunifolium* (black haw), while the woody vine *Parthenocissus quinquefolia* (Virginia creeper) was also common (Tables 1 and 8). During the fall survey the dominant herbaceous species of the ground layer included *Sanicula odorata* (common black snakeroot), *Viola sororia* (woolly blue violet), *Antenoron virginianum* (Virginia knotweed), and *Galium concinnum* (shining bedstraw) (Table 8). During the spring survey the dominant ground layer species were *Podophyllum peltatum* (Mayapple), *Dentaria laciniata* (toothwort), and *Circaea lutetiana* (enchanter's nightshade) along with the same dominant species documented in the fall survey.

Old growth dry-mesic savanna: Located on the flat uplands adjacent to the mesic ravine, this small savanna was less than one ha in size. The overstory was dominated by widely spaced open-grown individuals of *Quercus alba* that averaged 80 stems/ha with an average diameter of 67.1 cm dbh, an average basal area of 30.124 m^2/ha, and an IV of 165.2 (Table 3). Only a few other tree species exceeded 25 cm dbh, all with only a few stems/ha. *Acer saccharum* dominated the seedling and sapling categories though many other trees and a few shrub species were common (Table 3). In contrast, *Q. alba* was poorly represented in the sapling categories with no individuals being recorded. The extensive sapling understory of *A. saccharum* has developed since the picnic area was abandoned when the preserve was dedicated in 1979.

Mesic ravine upland forest: In the eastern part of the preserve is a mesic ravine dominated by mature second growth upland forest. Oriented northwest/southeast the SW- and NE-facing slopes were dominated by *Acer saccharum,* which accounted for nearly half of the stems/ha and more than one-third of the basal area (Tables 4 and 5). *Quercus alba* was second in IV on both slopes while most of the remainder comprised mesic species commonly associated with deep ravines in east-central Illinois. *Acer saccharum* accounted for more than half of the woody seedlings and saplings in this ravine.

Southern flatwood forest/ephemeral pond: This small community located near the southwestern edge of MFWNP is less than one ha in size. *Quercus bicolor* (swamp white oak) dominated the overstory with an IV of nearly 139 and accounted for nearly 60% of the stems/ha and 85% of the basal area in the pond. *Quercus alba* was fairly common with an IV of 24.2 (Table 6). Swamp white oak was the only tree species found in the standing water, the other species were confined to the edges of the ephemeral pond or to slightly elevated areas. Woody seedlings and saplings were nearly absent from the ephemeral pond, but some were occasionally encountered in slightly elevated areas. Herbaceous vegetation was sparse, probably due to the presence of standing water and dense shade from the overstory.

Immature second growth dry-mesic upland forest: This immature second growth forest is located near the center of the preserve and had been heavily harvested for timber 70 to 80 years ago (Wallace 1975). Tree species composition was similar to the mature second growth forest in the western part of MFWNP. Tree density averaged 436 stems/ha with the large majority of the individuals less than 35 cm dbh. *Quercus alba* was the dominant overstory species with 162 stems/ha, a basal area of 11.771 m^2/ha, and an IV of 76.9 (Table 7). *Carya ovata* (shagbark hickory) was second in importance with an IV of 53.1, followed by *Quercus rubra* (red oak) and *Q. velutina* with IV's of 28.4 and 13.0, respectively. All other tree species had IVs of less than 10. Dead-standing individuals averaged 55 stems/ha with an average basal area of 1.527 m^2/ha (Table 2). Tree seedlings and saplings were relatively common, but numerous shrubs dominated the woody understory with *Viburnum prunifolium* (black haw) being the most important (Table 7).

The woody understory of the immature second growth upland forest was dominated by a few tree seedlings and shrubs with *Viburnum prunifolium*, *Fraxinus americana*, *Viburnum recognitum* (smooth arrowwood) common along with the woody vine *Parthenocissus quinquefolia* (Tables 7 and 9). During the fall survey the dominant herbaceous species of the ground layer included *Antenoron virginianum*, *Carex* spp. (sedges), *Sanicula odorata*, and *Viola sororia* (Table 9). During the spring survey the ground layer vegetation included *Podophyllum peltatum*, *Prenanthes altissima* (tall white lettuce), *Dentaria laciniata*, and

various species of *Carex* along with the same dominant species found during the fall survey.

DISCUSSION

Wallace (1975) studied the composition and structure of the forest vegetation at MFWNP during the 1970s; at that time the MFWNP had a total stand density of 477.61 stems/ha, a total basal area of 25.64 m^2/ha, with 27 tree and shrub species encountered. Q*uercus alba* was the dominant species, with an IV of 75.34 (total possible 300), average of 135.71 stems/ha and a basal area of 7.96 m^2/ha. *Q. velutina* was second in importance (IV of 36.61), followed by *Acer saccharum* (IV of 35.47), *Q. rubra* (IV of 24.70), *Carya ovata* (IV of 23.16), and *Fraxinus americana* (IV of 21.82). Wallace (1975) also determined the average age of the trees in each community based on increment borings (at 1.37 meters) of the leading dominant species ≥9 cm dbh. Average tree age was the lowest in the immature second growth dry-mesic upland forest, and highest in the mesic ravine forest where some of the largest trees had 124 annual rings when surveyed in 1974. In the upland forests tree age averaged 48 annual rings in the immature upland forest and 62 annual rings in the more mature upland forest.

Mature second growth dry-mesic upland forest: In this forest type Wallace (1975) recorded 468 stems/ha with a basal area of 28.45 m^2/ha of which *Quercus alba* (IV of 162.54), *Q. velutina* (IV of 31.58), and *Acer saccharum* (IV of 26.75) accounted for 74% of the total IV. In 2002 tree density averaged 353 stems/ha with a basal area of 32.995 m^2/ha. The dominants remained the same as those observed by Wallace (1975) and accounted for 73% of the total IV. The general trend over the past 25 years at the MFWNP has been a decrease in stems/ha with a corresponding increase in basal area/ha, whereas the composition of the overstory changed slightly.

Old growth dry-mesic savanna: When Wallace (1975) conducted his study at MFWNP, the savanna was maintained as a picnic area. Many of the large open-grown white oaks are still present, which now average 80 stems/ha. The picnic area is no longer maintained and the major change in this community has been the explosive increase of a woody understory dominated by *Acer saccharum, Fraxinus americana, Prunus serotina,* and *Sassafras albidum* (Table 3).

Mesic ravine upland forest: Wallace (1975) described an *Acer saccharium-Tilia americana* community with small inclusions of a *Quercus rubra-Quercus alba* community in the steep ravines on the southwestern and western edges of MFWNP. Found exclusively within these steep ravines, this community averaged 447 trees/ha with an average basal area of 24.45 m^2/ha (Wallace 1975); *Acer saccharum* was the dominant species with an IV of 96.58, followed by *Tilia americana* (IV of 40.51), *Quercus alba* (IV of 33.97), and *Q. rubra* (IV of 25.68). During the present survey *A. saccharum* was the dominant species, whereas *Q. alba* was second in IV (Tables 4 and 5). *Tilia americana* and *Q. rubra* were reduced in importance, but still were common forest components. Also, *A. saccharum* continued to dominate the understory, accounting for more than half of the seedlings and saplings.

Southern flatwood forest/ephemeral pond: This community, which is restricted to a shallow depression often filled with water to 0.5 meters in depth from February to June, was dominated by *Quercus bicolor*. Two other species (*Carya ovata* and *Fraxinus americana*) were present at the edges of the depression (Wallace 1975). During the present study similar results were obtained though we recorded a few individuals of *Q. alba, Q. rubra,* and *Ulmus americana* in the pond that were not recorded by Wallace (1975).

Immature second growth dry-mesic upland forest: In 1974 the immature second growth dry-mesic upland forest trees averaged 525 stems/ha with a basal area of 20.68 m^2/ha. *Carya ovata* ranked first in importance (IV of 65.6) followed by *Quercus imbricaria* (shingle oak) and *Q. alba* (Wallace 1975). In this forest community in 2002, tree density averaged 436 stems/ha and the basal area averaged 29.68 m^2/ha. A shift in species dominance also occurred in the past 25 years; *Q. alba* became dominant, and along with *C. ovata,* accounted for 65% of the total IV (Table 7). *Quercus imbricaria* was poorly represented, having been replaced by *Q. rubra* and *Q. velutina*. A relatively long distance to a seed source at the time of logging

probably explains a lower importance of *Acer saccharum* in this community.

Successional trends: Wallace (1975) did not find *Asimina triloba* (pawpaw) or *Lindera benzoin* (spicebush) at MFWNP. Both may be recent arrivals, but it was more likely that these two species were scattered and uncommon on the preserve in the early 1970s. *Asimina triloba* is fire-sensitive, and when top-killed sprouts readily, often requiring two or more burns before dying (Larimore et al. 2003). *Lindera benzoin* is also easily top-killed by fire but re-sprouts rapidly. The absence of fire since the site became a dedicated nature preserve has probably been important in the increased presence of these two species as well as *Acer saccharum* and *Viburnum prunifolium*. These fire-sensitive, shade-tolerant species will probably continue to increase in importance in the future.

The upland forests of MFWNP have been undergoing substantial changes during the past 50–60 years. We have no definite evidence that fires were used in this forest before being dedicated as a nature preserve, but burning of grazing areas was common in Illinois during the early and middle 1900s (Miller 1920). With the absence of fire, the encroachment of mesic, fire-sensitive, shade-tolerant woody species, such as *Acer saccharum* and *Fagus grandiflora,* has been increasing dramatically (Ebinger 1986, Anderson 1991, Ebinger and McClain 1991, Abrams 1992, Packard 1993, McClain and Elzinga 1994). *Acer saccharum* continues to dominate the overstory and the woody understory of the ravine forests, and is an important component of the mature second growth dry-mesic upland forest where it is third in IV and dominates the large sapling layer. Also, a few saplings of *F. grandiflora* were encountered in the upland forests. This fire-sensitive species, however, is mostly restricted to the SE-facing slope of the ravine where it ranked fourth in importance. If this trend toward more mesic conditions continues, oak regeneration will likely decrease, as will the presence of other fire-resistant, shade-intolerant species. This increase in the number of *A. saccharum* and *F. grandifolia*, and the resulting decrease of oak regeneration, probably started with the reduction in landscape fires soon after Europeans settled the area (Ebinger and McClain 1991), and was accelerated with the cutting of the forest in the early 1900s and by fire suppression and the cessation of grazing 50–60 years ago.

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Table 1. Size class density (#/ha), basal area (m^2/ha), relative values, importance values, and average diameters (cm) of the woody species in a mature second growth dry-mesic upland forest at Middle Fork Woods Nature Preserve, Vermilion County, Illinois.

Species	Seedlings	Small Saplings	Large Saplings	Trees (#/ha)	Basal Area (m^2/ha)	Rel. Den.	Rel. Dom.	IV	Av. Diam (cm)
Quercus alba	560	--	--	138.5	16.762	39.2	50.8	90.0	37.3
Quercus velutina	--	--	--	44.5	6.823	12.6	20.7	33.3	42.9
Acer saccharum	600	100	360	65.5	1.277	18.6	3.9	22.5	15.0
Carya ovata	1120	20	22	28.0	1.602	7.9	4.9	12.8	24.6
Quercus rubra	--	--	--	15.0	2.467	4.3	7.5	11.8	43.2
Carya glabra	200	--	--	21.0	1.573	6.0	4.8	10.8	27.7
Fraxinus americana	6040	160	32	12.5	1.164	3.6	3.5	7.1	33.3
Tilia americana	--	20	6	6.5	0.232	1.9	0.7	2.6	18.8
Sassafras albidum	280	40	44	5.5	0.135	1.6	0.4	2.0	16.9
Ulmus americana	200	20	86	5.0	0.060	1.4	0.2	1.6	12.3
Quercus imbricaria	40	--	--	2.0	0.256	0.6	0.8	1.4	39.9
Ulmus rubra	--	--	42	2.5	0.126	0.7	0.4	1.1	24.3
Gleditsia triacanthos	40	--	--	1.0	0.255	0.3	0.8	1.1	56.4
Lindera benzoin	5360	340	--	--	--	--	--	--	--
Viburnum prunifolium	3240	400	--	--	--	--	--	--	--
Ribes missouriense	440	--	--	--	--	--	--	--	--
Viburnum recognitum	240	100	--	--	--	--	--	--	--
Zanthoxylum americanum	160	120	--	--	--	--	--	--	--
Lonicera maackii	120	--	--	--	--	--	--	--	--
Others (14 species)	2000	20	206	5.5	0.263	1.3	0.6	1.9	
Totals	20640	1340	798	353.0	32.995	100.0	100.0	200.0	

Table 2. Tree density (#/ha), basal area (m^2/ha), and average diameters (cm) of the dead-standing woody species in a mature second growth dry-mesic upland forest and an immature second growth dry-mesic upland forest at Middle Fork Woods Nature Preserve, Vermilion County, Illinois.

Species	Density (#/ha)	Basal Area (m^2/ha)	Average Diameter (cm)
Mature Second Growth Upland Forest			
Quercus alba	20.0	1.047	23.1
Quercus velutina	14.5	1.661	36.5
Fraxinus americana	2.0	0.139	26.9
Quercus rubra	2.0	0.133	27.1
Others	5.0	0.163	
Totals	43.5	3.143	
Immature Second Growth Upland Forest			
Quercus alba	37.0	0.914	17.5
Sassafras albidum	8.0	0.154	15.5
Quercus rubra	4.0	0.194	24.7
Carya ovata	4.0	0.176	21.7
Others	2.0	0.089	
Totals	55.0	1.527	

Table 3. Size class density (#/ha), basal area (m^2/ha), relative values, importance values, and average diameters (cm) of the woody species in an old growth dry-mesic savanna at Middle Fork Woods Nature Preserve, Vermilion County, Illinois.

Species	Seedlings	Small Saplings	Large Saplings	Trees (#/ha)	Basal Area (m^2/ha)	Rel. Den.	Rel. Dom.	IV	Av. Diam. (cm)
Quercus alba	750	--	--	80.0	30.124	69.1	96.1	165.2	67.1
Acer saccharum	40250	12250	425	12.0	0.156	10.4	0.5	10.9	12.8
Fraxinus americana	5750	2500	238	8.0	0.376	6.9	1.2	8.1	21.6
Ulmus rubra	1250	--	25	4.0	0.400	3.4	1.3	4.7	35.7
Tilia americana	--	--	--	4.0	0.152	3.4	0.5	3.9	22.0
Juglans nigra	--	--	--	4.0	0.080	3.4	0.2	3.6	16.1
Ostrya virginiana	1000	--	25	4.0	0.064	3.4	0.2	3.6	14.2
Carya ovata	2250	375	--	--	--	--	--	--	--
Sassafras albidum	2000	125	375	--	--	--	--	--	--
Prunus serotina	750	875	300	--	--	--	--	--	--
Celtis occidentalis	--	--	13	--	--	--	--	--	--
Viburnum prunifolium	6750	1125	25	--	--	--	--	--	--
Viburnum recognitum	500	500	75	--	--	--	--	--	--
Elaeagnus umbellata	250	--	25	--	--	--	--	--	--
Lonicera maackii	250	--	25	--	--	--	--	--	--
Totals	61750	17750	1551	116.0	31.352	100.0	100.0	200.0	

Table 4. Size class density (#/ha), basal area (m^2/ha), relative values, importance values, and average diameters (cm) of the woody species in a SW-facing mesic ravine upland forest at Middle Fork Woods Nature Preserve, Vermilion County, Illinois.

Species	Seed-lings	Small Sap-Lings	Large Sap-lings	Trees (#/ ha)	Basal Area (m^2/ ha)	Rel. Den.	Rel. Dom.	IV	Av. Diam. (cm)
Acer saccharum	79600	2900	260	120.0	9.676	46.4	37.3	83.7	29.8
Quercus alba	2000	--	--	40.0	7.296	15.5	28.1	43.6	45.7
Populus grandidentata	--	--	--	30.0	1.458	11.6	5.6	17.2	24.5
Fagus grandifolia	600	200	20	16.0	1.938	6.2	7.5	13.7	35.9
Quercus rubra	200	--	--	12.0	1.722	4.7	6.6	11.3	37.9
Tilia americana	--	--	10	6.0	1.006	2.2	3.9	6.1	42.5
Fraxinus americana	8200	1000	--	4.0	0.974	1.6	3.8	5.4	49.5
Juglans nigra	--	--	--	6.0	0.262	2.2	1.0	3.2	23.5
Quercus velutina	--	--	--	4.0	0.408	1.6	1.6	3.2	35.5
Carya ovata	1000	--	--	4.0	0.262	1.6	1.0	2.6	28.8
Quercus muhlenbergii	--	--	--	2.0	0.388	0.8	1.5	2.3	49.7
Ulmus rubra	--	--	--	4.0	0.174	1.6	0.7	2.3	22.1
Sassafras albidum	1400	100	--	4.0	0.162	1.6	0.6	2.2	22.4
Prunus serotina	3400	--	--	2.0	0.150	0.8	0.6	1.4	30.9
Ulmus americana	200	--	--	2.0	0.036	0.8	0.1	0.9	15.2
Ostrya virginiana	2600	300	90	2.0	0.018	0.8	0.1	0.9	10.5
Carya cordiformis	2000	500	--	--	--	--	--	--	--
Cornus florida	400	--	--	--	--	--	--	--	--
Viburnum recognitum	1200	--	--	--	--	--	--	--	--
Elaeagnus umbellata	600	100	--	--	--	--	--	--	--
Lindera benzoin	200	100	--	--	--	--	--	--	--
Morus rubra	--	100	--	--	--	--	--	--	--
Totals	103600	5300	380	258.0	25.930	100.0	100.0	200.0	

Table 5. Size class density (#/ha), basal area (m^2/ha), relative values, importance values, and average diameters (cm) of the woody species in a NE-facing mesic ravine upland forest at Middle Fork Woods Nature Preserve, Vermilion County, Illinois.

Species	Seed-lings	Small Sap-lings	Large Sap-lings	Trees (#/ ha)	Basal Area (m^2/ha)	Rel. Den.	Rel. Dom.	IV	Av. Diam. (cm)
Acer saccharum	15800	2600	660	128.0	11.024	65.3	44.4	109.7	29.1
Quercus alba	--	--	--	12.0	5.494	6.2	22.2	28.4	76.0
Juglans nigra	--	--	--	12.0	2.434	6.2	9.8	16.0	48.8
Ulmus rubra	--	--	20	16.0	0.266	8.2	1.1	9.3	14.3
Quercus muhlenbergii	--	--	--	4.0	1.376	2.0	5.6	7.6	66.1
Carya glabra	400	--	--	4.0	1.208	2.0	4.9	6.9	62.0
Carya ovata	400	--	--	6.0	0.690	3.1	2.8	5.9	33.9
Quercus rubra	--	--	--	2.0	1.044	1.0	4.2	5.2	81.5
Sassafras albidum	--	--	--	4.0	0.596	2.0	2.4	4.4	43.6
Carya cordiformis	--	100	--	2.0	0.352	1.0	1.4	2.4	47.4
Tilia americana	--	--	--	2.0	0.182	1.0	0.7	1.7	34.0
Fraxinus americana	9000	--	--	2.0	0.102	1.0	0.4	1.4	25.4
Ulmus americana	--	--	--	2.0	0.020	1.0	0.1	1.1	11.1
Ostrya virginiana	200	--	20	--	--	--	--	--	--
Celtis occidentalis	--	--	10	--	--	--	--	--	--
Asimina triloba	2400	1300	50	--	--	--	--	--	--
Ribes missouriense	200	--	--	--	--	--	--	--	--
Totals	28400	4000	760	196.0	24.788	100.0	100.0	200.0	

Table 6. Size class density (#/ha), basal area (m^2/ha), relative values, importance values, and average diameters (cm) of the woody species in a southern flatwood forest/ephemeral pond community at Middle Fork Woods Nature Preserve, Vermilion County, Illinois.

Species	Seed-lings	Small Sap-lings	Large Sap-lings	Trees (#/ ha)	Basal Area (m^2/ ha)	Rel. Den.	Rel. Dom.	IV	Av. Diam. (cm)
Quercus bicolor	--	--	--	120.0	24.196	58.8	79.9	138.7	46.7
Quercus alba	--	--	--	20.0	4.356	9.8	14.4	24.2	51.3
Carya ovata	--	--	10	28.0	0.580	13.7	1.9	15.6	15.5
Ulmus americana	--	100	250	28.0	0.468	13.7	1.5	15.2	14.3
Quercus rubra	--	--	--	4.0	0.372	2.0	1.2	3.2	34.4
Fraxinus lanceolata	2000	100	10	4.0	0.328	2.0	1.1	3.1	32.2
Carpinus caroliniana	400	100	40	--	--	--	--	--	--
Crataegus pruinosa	--	--	20	--	--	--	--	--	--
Ulmus rubra	--	--	20	--	--	--	--	--	--
Viburnum prunifolium	600	--	20	--	--	--	--	--	--
Viburnum recognitum	400	300	120	-	--	--	--	--	--
Totals	3400	600	490	204.0	30.300	100.0	100.0	200.0	

Table 7. Size class density (#/ha), basal area (m^2/ha), relative values, importance values, and average diameters (cm) of the woody species in an immature second growth dry-mesic upland forest at Middle Fork Woods Nature Preserve, Vermilion County, Illinois.

Species	Seed-lings	Small Sap-lings	Large Sap-lings	Trees (#/ ha)	Basal Area (m^2/ ha)	Rel. Den.	Rel. Dom.	IV	Av. Diam. (cm)
Quercus alba	--	--	--	162.0	11.771	37.2	39.7	76.9	29.7
Carya ovata	1800	--	20	141.0	6.162	32.3	20.8	53.1	22.5
Quercus rubra	200	--	--	45.0	5.368	10.3	18.1	28.4	37.6
Quercus velutina	--	--	--	21.0	2.445	4.8	8.2	13.0	37.3
Fraxinus lanceolata	9800	900	20	18.0	1.507	4.1	5.1	9.2	31.5
Carya tomentosa	--	--	--	9.0	0.348	2.1	1.2	3.3	21.3
Quercus imbricaria	--	--	--	6.0	0.562	1.4	1.9	3.3	33.6
Ulmus americana	--	--	100	9.0	0.178	2.1	0.6	2.7	15.3
Acer saccharum	200	--	80	8.0	0.080	1.8	0.3	2.1	11.2
Sassafras albidum	400	200	80	6.0	0.145	1.4	0.5	1.9	16.7
Tilia americana	--	--	--	4.0	0.332	0.9	1.0	1.9	26.1
Carya glabra	--	--	--	3.0	0.202	0.7	0.7	1.4	28.4
Quercus bicolor	--	--	--	1.0	0.369	0.2	1.2	1.4	68.5
Carya cordiformis	--	--	--	2.0	0.130	0.5	0.4	0.9	28.2
Gleditsia triacanthos	200	--	--	1.0	0.081	0.2	0.3	0.5	32.2
Prunus serotina	800	--	40	--	--	--	--	--	--
Viburnum prunifolium	21200	4400	40	--	--	--	--	--	--
Viburnum recognitum	800	100	--	--	--	--	--	--	--
Zanthoxylum americanum	800	400	--	--	--	--	--	--	--
Corylus americana	200	--	--	--	--	--	--	--	--
Lindera benzoin	200	--	--	--	--	--	--	--	--
Crataegus pruinosa	--	--	30	--	--	--	--	--	--
Totals	36600	6000	410	436.0	29.680	100.0	100.0	200.0	

Table 8. Frequency (%), average cover, relative frequency, relative cover, and importance values of the ground layer species encountered in early fall in a mature second growth dry-mesic upland forest at Middle Fork Woods Nature Preserve, Vermilion County, Illinois. Only species with an importance value of ≥1.0 are listed.

Species	Frequency%	Mean Cover	Relative Frequency	Relative Cover	IV
Lindera benzoin	62	5.49	14.2	55.6	69.8
Sanicula odorata	86	1.03	19.8	10.4	30.2
Viola sororia	36	0.28	8.3	2.8	11.1
Fraxinus americana	30	0.40	6.9	4.1	11.0
Parthenoicissus quinquefolia	34	0.27	7.8	2.7	10.5
Carya ovata	22	0.51	5.1	5.2	10.3
Antenoron virginianum	32	0.26	7.4	2.6	10.0
Galium concinnum	12	0.45	2.7	4.6	7.3
Ulmus spp.	18	0.09	4.1	0.9	5.0
Carex spp.	12	0.16	2.7	1.6	4.3
Viburnum prunifolium	12	0.16	2.7	1.6	4.3
Rubus spp.	8	0.04	1.8	0.4	2.2
Carya cordiformis	4	0.12	0.9	1.2	2.1
Phryma leptostachya	6	0.03	1.4	0.3	1.7
Actaea pachypoda	4	0.07	0.9	0.7	1.6
Lonicera maackii	4	0.07	0.9	0.7	1.6
Solidago ulmifolia	4	0.07	0.9	0.7	1.6
Dioscorea villosa	4	0.02	0.9	0.2	1.1
Ageratina altissima	2	0.06	0.5	0.6	1.1
Geum canadense	4	0.02	0.9	0.2	1.1
Oxalis stricta	4	0.02	0.9	0.2	1.1
Quercus velutina	4	0.02	0.9	0.2	1.1
Ribes missouriense	2	0.06	0.5	0.6	1.1
Scutellaria incana	2	0.06	0.5	0.6	1.1
Vitis spp.	4	0.02	0.9	0.2	1.1
Others (11 species)		0.11	5.5	1.1	6.6
Totals		9.89	100.0	100.0	200.0
Average bare ground/litter		85.45			

Table 9. Frequency (%), average cover, relative frequency, relative cover, and importance values of the ground layer species encountered in early fall in an immature second growth dry-mesic upland forest at Middle Fork Woods Nature Preserve, Vermilion County, Illinois. Only species with an importance value of ≥1.0 are listed.

Species	Frequency%	Mean Cover	Relative Frequency	Relative Cover	IV
Viburnum prunifolium	68	7.22	8.9	33.9	42.8
Antenoron virginianum	78	3.04	10.2	14.4	24.6
Fraxinus americana	70	2.70	9.1	12.8	21.9
Carex spp.	54	2.22	7.0	10.5	17.5
Sanicula odorata	68	0.99	8.9	4.8	13.7
Parthenocissus quinquefolia	56	0.68	7.3	3.2	10.5
Carya ovata	38	0.83	4.9	3.9	8.8
Viola sororia	44	0.27	5.7	1.3	7.0
Viburnum recognitum	28	0.19	3.6	0.9	4.5
Sassafras albidum	6	0.66	0.8	3.1	3.9
Galium concinnum	20	0.10	2.6	0.5	3.1
Aster lanceolatus	18	0.09	2.3	0.4	2.7
Bromus pubescens	12	0.26	1.5	1.2	2.7
Solidago ulmifolia	14	0.17	1.8	0.8	2.6
Rubus spp	12	0.21	1.5	1.0	2.5
Toxicodendron radicans	16	0.08	2.0	0.4	2.4
Ageratina altissima	8	0.24	1.0	1.1	2.1
Phlox divaricata	12	0.06	1.5	0.3	1.8
Prunus serotina	12	0.06	1.5	0.3	1.8
Stellaria longifolia	6	0.13	0.8	0.6	1.4
Geum canadense	8	0.04	1.0	0.2	1.2
Osmorhiza spp.	8	0.04	1.0	0.2	1.2
Quercus imbricaria	8	0.04	1.0	0.2	1.2
Ulmus spp.	6	0.08	0.8	0.4	1.2
Podophyllum peltatum	4	0.12	0.5	0.6	1.1
Others (29 species)		0.77	12.8	3.0	15.8
Totals		21.29	100.0	100.0	200.0
Average bare ground/litter		79.45			

APPENDIX I

Vascular plant species encountered at the Middle Fork Woods Nature Preserve, Vermilion County, Illinois are listed alphabetically by family under major plant groups. All specimens were collected by R.L. Larimore and are deposited in the Illinois Natural History Survey herbarium, Champaign (ILLS). An asterisk indicates non-native (exotic) species (*). After the binomial, authority, and author's collecting number, the community number(s) where the species were collected or observed are given. (1 = mature second growth dry-mesic upland forest; 2 = dry-mesic savanna; 3 = mesic ravine forest; 4 = southern flatwood forest/ephemeral pond; 5 = immature second growth dry-mesic upland forest; 6 = east-facing bluff above river (dry upland); 7 = perennial stream; 8 = west-facing bluff above creek (dry upland).

SPHENOPHYTA

EQUISETACEAE
Equisetum arvense L., 262;3
Equisetum hyemale L., 263;3

PTERIDOPHYTA

ASPLENIACEAE
Asplenium platyneuron (L.) Oakes, 482;6

DRYOPTERIDACEAE
Athyrium filix-femina (L.) Martens, 179;1
Cystopteris protrusa (Weatherby) Blasdell, 187, 495;8
Polystichum acrostichoides (Michx.) Schott, 259, 733;2,3,5,6,8

ONOCLEACEAE
Onoclea sensibilis L., 44;1,5

OPHIOGLOSSACEAE
Botrychium virginianum (L.) Sw., 127;1,3,5
Ophioglossum vulgatum L., 741;1

PTERIDACEAE
Adiantum pedatum L., 258;3

THELYPTERIDACEAE
Phegopteris hexagonoptera (Michx.) Fee, 552, 721;1,5

CONIFEROPHYTA
CUPRESSACEAE
Juniperus virginiana L., 730;1,2,5,6,8

ANTHOPHYTA – MONOCOTYLEDONAE

ARACEAE
Arisaema dracontium (L.) Schott, 99;1,3,5
Arisaema triphyllum (L.) Schott, 102;1,3,5

COMMELINACEAE
**Commelina communis* L., 461;7
Tradescantia subaspera Ker, 253;7
Tradescantia virginiana L., 163, 184;6,8

CYPERACEAE
Carex albicans Willd., 68;6
Carex albursina Sheldon, 85;3
Carex amphibola Steud., 155;5
Carex blanda Dewey, 103;1
Carex buxbaumii Wahl., 144;4
Carex cephalophora Muhl., 75, 90;6,7
Carex conjuncta Boott, 135, 735;3,7
Carex davisii Schwein. & Torr., 77;6
Carex digitalis Willd., 86A, 112;1,3
Carex festucacea Schk., 729;3
Carex frankii Kunth, 354;7
Carex gracilescens Steud., 40, 79;4,5
Carex gracillima Schwein., 80, 743;4
Carex granularis Muhl., 151;5
Carex grisea Wahl., 78, 88;3,4
Carex hirsutella Mack., 124;1
Carex hirtifolia Mack., 76;6
Carex hitchcockiana Dewey, 125;1
Carex jamesii Schwein., 108;1
Carex laxiculmis Schwein., 88A, 154, 158;3
Carex molesta Mack., 134, 724;7
Carex normalis Mack., 744;5
Carex pensylvanica Lam., 105;1,2,5,6,8
Carex radiata (Wahl.) Small, 82;4
Carex rosea Schk., 72, 111, 161;1,5,6,8
Carex shortiana Dewey, 145;5
Carex sparganioides Muhl., 70, 178;6
Carex squarrosa L., 149;5
Carex vulpinioidea Michx., 129;7
Cyperus odoratus L., 306;7
Cyperus squarrosus L., 299, 333;7
Cyperus strigosus L., 455;7
Eleocharis erythropoda Steud., 130;7
Hemicarpha micrantha (Vahl) Pax, 465, 526;7

DIOSCOREACEAE
Dioscorea villosa L., 505;5

IRIDACEAE
Sisyrinchium angustifolium Mill., 152;5

JUNCACEAE
Juncus tenuis Willd., 324;6,8

LILIACEAE
Allium burdickii (Hanes) A.G. Jones, 178a;1,2,3,5,6,8
Allium canadense L., 81;1,2,3,5,6,8
Polygonatum commutatum (Schult.) A. Dietr., 739;8
Smilacina racemosa (L.) Desf., 727;3
Trillium flexipes Raf., 34;3
Trillium recurvatum Beck, 45;1,2,3,5,6,8
Uvularia grandiflora Sm., 69;3

ORCHIDACEAE
Corallorhiza odontorhiza (Willd.) Nutt., 484;5
Liparis liliifolia (L.) Rich., 169, 323;6

POACEAE
Agrostis gigantea Roth, 277;7
Agrostis perennans (Walt.) Tuckerm., 316, 550;1,2,3,5,6,8
Brachyelytrum erectum (Roth) P. Beauv., 185;3
Bromus latiglumis (Shear) Hitchc., 284;7
Bromus pubescens Muhl., 174;1,2,5,6,8
Chasmanthium latifolium (Michx.) Yates, 283;7
Cinna arundinacea L., 363;1,2,3,4,5,6,7,8
**Dactylis glomerata* L., 146;5
Danthonia spicata (L.) Roem. & Schultes, 269;6,7
Diarrhena obovata (Gl.) Brandenburg, 260;3,7
Dichanthelium acuminatum (Sw.) Gould & Clark, 121, 270, 181;1,5,6
Dichanthelium clandestinum (L.) Gould, 137, 177;3,7
Digitaria filiformis (L.) Koel., 463;7
**Digitaria sanguinalis* (L.) Scop., 527;7
**Echinochloa crus-galli* (L.) P. Beauv., 295;7
Elymus canadensis L., 346;7
Elymus hystrix L., 173;1,2,3,4,5,6,7,8
Elymus villosus Muhl., 172;5
Elymus virginicus L., 138;3,7
Eragrostis frankii C.A. Meyer, 489, 533;7
Eragrostis hypnoides (Lam.) BSP., 339;7
Eragrostis pectinacea (Michx.) Nees, 464, 490;7
**Festuca arundinacea* Schreb., 140;7
Festuca subverticillata (Pers.) E.B. Alexeev. 147;1,2,5,6,8
Glyceria striata (Lam.) Hitchc., 150;1,4,5
Leersia oryzoides (L.) Swartz, 508;7
Leersia virginica Willd., 366;1,3,4,5,
Leptochloa fascicularis (Lam.) Gray, 509;7
Muhlenbergia frondosa (Poir.) Fern., 454, 486;7
Muhlenbergia sobolifera (Muhl.) Trin., 443;3
Muhlenbergia tenuiflora (Willd.) BSP., 485;7
Panicum capillare L., 528;7
Panicum dichotomiflorum Michx., 294;7
Panicum virgatum L., 349;7
Phalaris arundinacea L., 132;7
**Phleum pratense* L., 275;7
**Poa compressa* L., 122, 180;6
**Poa pratensis* L., 63;6
Poa sylvestris A. Gray, 87;3
**Setaria faberi* R.A.W. Herrm., 488;7
**Setaria glauca* (L.) P. Beauv., 342;7
**Setaria viridis* (L.) P. Beauv., 293;7
Sorghastrum nutans (L.) Nash, 467;7
Sphenopholis obtusata (Michx.) Scribn., 148;5

POTAMOGETONACEAE
**Potamogeton crispus* L., 535;7

SMILACACEAE
Smilax ecirrhata Kunth, 723;1,3,5,6,8
Smilax lasioneuron Hook., 732;6
Smilax tamnoides L., 445;1,2,3,4,5,6,7,8

ANTHOPHYTA – DICOTYLEDONAE

ACANTHACEAE
Justicia americana (L.) Vahl, 521;7
Ruellia strepens L., 460;7

ACERACEAE
Acer negundo L., 13;3,7
Acer nigrum Michx. f., 497;3
Acer saccharinum L., 297;7
Acer saccharum Marsh., 483, 538;1,2,3,4,5,6,8

AMARANTHACEAE
Amaranthus tuberculatus (Moq.) Sauer, 512, 513;7

ANACARDIACEAE
Rhus glabra L.,291, 352, 524;7
Toxicodendron radicans (L.) Kuntze, 115;1,2,3,4,5,6,7,8

ANNONACEAE
Asimina triloba (L.) Dunal, 33;3

APIACEAE
Chaerophyllum procumbens (L.) Crantz, 92;3,7

Cryptotaenia canadensis (L.) DC., 126;3,7
**Daucus carota* L., 278;7
Erigenia bulbosa (Michx.) Nutt., 1;3,6
Osmorhiza claytonii (Michx.) C.B. Clarke, 73;1,3,5,7
Osmorhiza longistylis (Torr.) DC., 740;3
Oxypolis rigidior (L.) Raf., 504;5
Sanicula canadensis L., 255;1,2,3,5,6,7,8
Sanicula odorata (Raf.) Pryer & Phillippe, 100, 238;1,2,3,5,6,7,8
Sanicula trifoliata Bickn., 265;3
Thaspium barbinode (Michx.) Nutt., 450;3

APOCYNACEAE
Apocynum cannabinum L., 353;7

ARALIACEAE
Panax quinquefolius L., 266;1,3,5

ARISTOLOCHIACEAE
Aristolochia serpentaria L., 186;3,6,8
Asarum canadense L., 53, 98;1,3,5,6,8

ASCLEPIADACEAE
Asclepias exaltata L., 395;3
Asclepias syriaca L., 726;7

ASTERACEAE
Ageratina altissima (L.) R.M. King & H. Rob., 330;1,2,3,4,5,6,7,8
Ambrosia artemisiifolia L., 308;7
Ambrosia trifida L., 309;7
Antennaria plantaginifolia (L.) Hook., 64;6,8
Aster cordifolius L., 543, 546;3,5,6,8
Aster lanceolatus Willd., 331, 530;7
Aster lateriflorus (L.) Britt., 502,549;3,5
Aster shortii Lindl., 328;6
Bidens cernua L., 337;7
Bidens connata Muhl., 534;7
Bidens frondosa L., 547;3
Bidens vulgata Greene, 369;1,5
Conyza canadensis (L.) Cronq., 469;7
Eclipta prostrata (L.) L., 313;7
Erechtites hieracifolia (L.) Raf., 478;4
Erigeron annuus (L.) Pers., 118, 251;6,7
Erigeron philadelphicus L., 93;7
Eupatoriadelphus purpureus (L.) R. M. King & H. Rob., 296;7
Eupatorium perfoliatum L., 545; 3
Eupatorium serotinum Michx., 357;7
Helenium autumnale L., 289, 332;7
Heliopsis helianthoides (L.) Sweet, 247;7
Lactuca floridana (L.) Gaertn., 452;3
Polymnia canadensis L., 517;7
Prenanthes altissima L., 493;1,5
Rudbeckia laciniata L., 358;7
Rudbeckia triloba L., 356;7
Senecio glabellus Poir., 91;7
Senecio obovatus Muhl., 110, 580;8
Silphium perfoliatum L., 336;7
Solidago caesia L., 506;1,3,5,6,7,8
Solidago canadensis L., 503;5
Solidago flexicaulis L., 541;3,6,8
Solidago gigantea Ait., 286, 338;7
Solidago ulmifolia Muhl., 329, 499;5,6,8
**Taraxacum officinale* Weber, 10;7
Verbesina alternifolia (L.) Britt., 285, 458;7
Vernonia gigantea (Walt.) Trel., 314;5
Xanthium strumarium L. 312;7

BALSAMINACEAE
Impatiens capensis Meerb., 448;1,3,4,5,7,8

BERBERIDACEAE
Caulophyllum thalictroides (L.) Michx., 84;3
Podophyllum peltatum L., 97;1,2,3,5,6,8

BIGNONIACEAE
**Catalpa bignonioides* Walt., 143;7

BORAGINACEAE
Mertensia virginica (L.) Pers., 11;3,7
Myosotis macrosperma Engelm., 120;6

BRASSICACEAE
**Alliaria petiolata* (Bieb.) Cavara & Grande, 48;1,2,3,5,6,7,8
Arabis canadensis L., 731;3
Arabis laevigata (Willd.) Poir., 162;8
Arabis shortii (Fern.) Gl., 83;3
**Barbarea vulgaris* R. Br. 36;7
**Brassica nigra* (L.) Koch, 355;7
Cardamine douglassii (Torr.) Britt., 2;1,4,5
Cardamine parviflora L., 74, 722;1,4,5
Dentaria laciniata Muhl., 3;1,2,3,4,5,6,7,8
Iodanthus pinnatifidus (Michx.) Steud., 139, 456;7
Rorippa palustris (L.) Besser, 274;7
**Rorippa sylvestris* (L.) Besser, 246;7

CAESALPINIACEAE
Cercis canadensis L., 47, 304;2,5,6,7,8
Gleditsia triacanthos L., 300;7

CAMPANULACEAE
Campanulastrum americanum (L.) Small, 280;3,5,6,7,8
Lobelia inflata L., 361;5

Lobelia siphilitica L., 290;7
Triodanis perfoliata (L.) Nieuwl., 119;6,7,8

CAPRIFOLIACEAE
**Lonicera japonica* Thunb., 368;1,3,5
**Lonicera maackii* (Rupr.) Maxim., 62, 248;6
**Lonicera morrowii* Gray, 71, 240;6
Lonicera reticulata Raf., 268;1,3,5,6,8
Sambucus canadensis L., 518;1,3,5,6,7,8
Symphoricarpos orbiculatus Moench, 439;1,5
Triosteum aurantiacum Bickn., 261, 327, 738;3
Viburnum prunifolium L., 39;1,2,5,6,8
Viburnum recognitum Fern., 165;1,4,5

CARYOPHYLLACEAE
**Cerastium fontanum* Baum, 117;6
Moehringia lateriflora (L.) Fenzl., 56;5
Silene stellata (L.) Ait. f., 236;3
Silene virginica L., 273;8
Stellaria longifolia Muhl., 55;5

CHENOPODIACEAE
**Atriplex patula* L., 514;7
**Chenopodium album* L., 519;7

CONVOLVULACEAE
Calystegia sepium (L.) R. Br., 359;7

CORNACEAE
Cornus drummondii C.A. Mey., 157, 321;3,5
Cornus florida L., 106;1,6,8

CORYLACEAE
Carpinus caroliniana Walt., 264;1,2,3,4,5,6,7,8
Corylus americana Walt., 347;5,7
Ostrya virginiana (Mill.) K. Koch, 440;1,2,3,5,6,8

CRASSULACEAE
Sedum ternatum Michx., 554;7

ELAEAGNACEAE
**Elaeagnus umbellata* Thunb., 66;5,6

EUPHORBIACEAE
Acalypha deamii (Weatherby) Ahles, 525;7
Acalypha rhomboidea Raf., 350, 472;7
Acalypha virginica L., 481;1,2,5,6,8
Chamaesyce maculata (L.) Small, 473;7
Chamaesyce nutans (Lag.) Small, 292;7

FABACEAE
Amorpha fruticosa L., 141;7
Desmodium glutinosum (Muhl.) A. Wood, 183;6
Desmodium nudiflorum (L.) DC., 272;8
**Melilotus albus* Medic., 250;7
**Robinia pseudoacacia* L., 745;5
**Securigera varia* (L.) Lassen, 462;7

FAGACEAE
Fagus grandifolia Ehrh., 401;1,2,3,5
Quercus alba L., 319;1,2,5,6,8
Quercus bicolor Willd., 325;4
Quercus imbricaria Michx., 320, 544;5
Quercus X leana Nutt., 317, 492, 501;5
Quercus macrocarpa Michx., 322;6,7
Quercus muhlenbergii Engelm., 396, 453, 496;3,6,8
Quercus rubra L., 480, 494;3,5,6,8
Quercus velutina Lam., 399, 498;1,5,6,8

FUMARIACEAE
Dicentra cucullaria (L.) Bernh., 5;3

GERANIACEAE
Geranium maculatum L., 41, 167;3,5,6,8

GROSSULARIACEAE
Ribes missouriense Nutt., 65;1,2,3,4,5,6,7,8

HIPPOCASTANACEAE
Aesculus glabra Willd., 449;1,3,5,6,7,8

HYDRANGEACEAE
Hydrangea arborescens L., 267;1,3,5,6,7,8

HYDROPHYLLACEAE
Ellisia nyctelea L., 61;3,6
Hydrophyllum appendiculatum Michx., 89;1,3,5
Hydrophyllum virginianum L., 742;1,5

JUGLANDACEAE
Carya cordiformis (Wangenh.) K. Koch, 474;1,2,3,4,5,6,7,8
Carya glabra (Mill.) Sweet, 441;1,5,6,8
Carya laciniosa (Michx.) Loud., 326;5
Carya ovata (Mill.) K. Koch, 315;1,2,4,5,6,8
Juglans nigra L., 479;3,5,6,7,8

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Blephilia hirsuta (Pursh) Bernh., 539;3
**Glechoma hederacea* L., 107;1,2,5,6,7,8
Lycopus americanus Muhl., 470;7
Lycopus virginicus L., 515;7
**Mentha arvensis* L., 548;3
**Prunella vulgaris* L., 364;5
Scutellaria incana Biehler, 241;5

Scutellaria lateriflora L., 471;7
Scutellaria ovata Hill, 182;5
Stachys tenuifolia Willd., 360;7
Teucrium canadense L., 244;7

LAURACEAE
Lindera benzoin (L.) Blume, 15;1,3,4,5
Sassafras albidum (Nutt.) Nees, 52, 303;1,2,5,6,8

LYTHRACEAE
Ammannia coccinea Rottb., 307;7

MAGNOLIACEAE
Liriodendron tulipifera L., 477;5

MENISPERMACEAE
Menispermum canadense L., 451;1,3,4,5,6,7,8

MOLLUGINACEAE
**Mollugo verticillata* L., 348;7

MONOTROPACEAE
Monotropa hypopithys L., 442;5

MORACEAE
**Maclura pomifera* (Raf.) Schneider, 457;3,7
**Morus alba* L., 511;7
Morus rubra L., 537;3

OLEACEAE
Fraxinus americana L., 318;1,5,6,8
Fraxinus lanceolata Borkh., 343;3,7

ONAGRACEAE
Circaea lutetiana L., 171;1,2,3,4,5,6,7,8

OROBANCHACEAE
Conopholus americana (L.) Wallr., 187, 495;1,2,3,5,6,8

OXALIDACEAE
Oxalis fontana Bunge, 170;5
Oxalis stricta L., 128;1,3
Oxalis violacea L., 109;6

PAPAVERACEAE
Sanguinaria canadensis L., 6;3,5,6,8

PASSIFLORACEAE
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PHRYMACEAE
Phryma leptostachya L., 254;1,3,5,6,8

PLANTAGINACEAE
Plantago rugelii Decne., 252;7

PLATANACEAE
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POLEMONIACEAE
Phlox divaricata L., 38;1,2,3,4,5,6,7,8
Phlox paniculata L., 281;7

POLYGALACEAE
Polygala senega L., 116;6

POLYGONACEAE
Antenoron virginianum (L.) Roberty & Vautier, 365;1,2,3,4,5,6,7,8
Fallopia scandens (L.) Holub, 446, 523;3,5
Persicaria cespitosa (Blume) Nakai, 301;7
Persicaria lapathifolia (L.) S. F. Gray, 311;7
Persicaria pensylvanica (L.) Small, 310;7
Persicaria punctata (Ell.) Small, 367, 529;3,4,7
**Persicaria vulgaris* Webb & Moq., 282;7
Rumex altissimus Wood, 142;7
**Rumex crispus* L., 136;7

PORTULACEAE
Claytonia virginica L., 4;1,2,3,4,5,6,7,8

PRIMULACEAE
Dodecatheon meadia L., 35;8
Lysimachia lanceolata Walt., 904;5
**Lysimachia nummularia* L., 468;7
Samolus parviflorus Raf., 520;7

RANUNCULACEAE
Actaea pachypoda Ell., 104;1,3,5
Anemone virginiana L., 239;3,6
Enemion biternatum Raf., 7;3,5,6,7,8
Hepatica americana (DC.) Ker, 14;3,6,8
Hydrastis canadensis L., 95, 734;1,2,5
Ranunculus abortivus L., 49;2,5,7
Ranunculus recurvatus Poir., 96;1,5
Ranunculus sceleratus L., 522;7
Ranunculus septentrionalis Poir., 37, 43;5,7
Thalictrum dasycarpum Fisch. & Lall, 447;3

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Agrimonia parviflora Sol., 475;3,4,5
Agrimonia pubescens Wallr., 362;1,5,6,8
Agrimonia rostellata Wallr., 271;1,5,6,8
Amelanchier arborea (Michx. f.) Fern., 176;5
Crataegus crus-galli L., 491;1,5
Crataegus pruinosa (Wendl.) K. Koch, 58;1,5
Geum canadense Jacq., 237;1,2,3,4,5,6,7,8

Geum vernum (Raf.) Torr. & Gray, 46;1,2,3,4,5,6,7,8
Malus coronaria (L.) Mill., 59;5
Potentilla simplex Michx., 168;1,2,3,5,6,8
Prunus serotina Ehrh., 57;1,2,5,6,8
**Rosa multiflora* Thunb., 131;1,2,3,5,6,7,8
Rosa setigera Michx., 487;7
Rubus flagellaris Willd., 166;1,5
Rubus occidentalis L., 476;1,3,4,5,6,7
Rubus pensilvanicus Poir., 133;1,3,4,5,6,7

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Galium aparine L., 50, 51, 160;1,2,3,4,5,6,7,8
Galium circaezans Michx., 123, 242;1,2,3,5,6,7,8
Galium concinnum Torr. & Gray, 60;1,2,3,4,5,6,8
Galium obtusum Bigel., 164, 257;1,3,4,5,6,7,8
Galium triflorum Michx., 243;1,2,3,5,6,7,8

RUTACEAE
Zanthoxylum americanum Mill., 175;1,2,5

SALICACEAE
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Populus grandidentata Michx., 398;5
Salix amygdaloides Anderss., 288;7
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Gratiola neglecta Torr., 256;4
Leucospora multifida (Michx.) Nutt., 341;7
Lindernia dubia (L.) Pennell, 466;7
Mimulus alatus Sol., 542;3
Mimulus ringens L., 340;7
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Scrophularia marilandica L., 459;7
**Verbascum thapsus* L., 334;7
Veronica peregrina L., 94;7

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Physalis subglabrata Mack. & Bush, 531;7
Solanum carolinense L., 276;
Solanum ptychanthum Dunal, 298, 351;7

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Staphylea trifolia L., 159;3,7

TILIACEAE
Tilia americana L., 400;3,5,6,8

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Celtis occidentalis L., 736;3
Ulmus americana L., 12;1,3,4,5,7
Ulmus rubra Muhl., 482a;1,3,5

URTICACEAE
Boehmeria cylindrica (L.) Sw., 510;3,7
Laportea canadensis (L.) Wedd., 536;3
Pilea pumila (L.) Gray, 516, 540;3,7
Urtica gracilis Ait., 737;3

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Notes

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A Division of the Illinois Department of Natural Resources

ISBN 978-1-882932-17-7